ECOLOGICAL MONOGRAPHS

Vol. 10 JULY, 1940 No. 3

Symposium

on

RELATION OF ECOLOGY TO HUMAN WELFARE—THE HUMAN SITUATION

Annual Meeting

of the

Ecological Society of America

at

Columbus, Ohio

December 27, 1939

CONTENTS

INTRODUCTORY NOTE

Many naturalists have for some time been concerned with the role which scientific work plays in modern society. The various efforts made to curb research, the practical difficulties of getting funds to conduct needed and urgent research from both private and public sources, the immense amount spent and/or wasted on so-called public defense, the misuse of funds for anti-social propaganda purposes, the effort made to discredit intelligence, the pressure of minor groups which are committed to outdated attitudes toward life and democratic freedom—all of these in the aggregate are enough to demand the serious attention of naturalists. Not only should they be on their guard, but as well should make a serious study of their own fundamental criterions of value, and to re-orient themselves and their work in modern society in order that they may be able to act more intelligently. As the ultimate tests of all values are social, this orientation involves the application of scientific methods to public welfare, and an intelligent social control, of both intelligence and emotion, in order to put emotional drive behind those procedures and policies that are of the greatest social value.

One of the best methods of assisting in this re-orientation is by the dispassionate discussion of the relations of a person's specialty in relation to the larger field, including its implications, and likewise to the extension of this same process to the integration of the "natural" and the "social" sciences, in order to facilitate the appreciation of their mutual interrelations and to obtain a proper balance between theory and practice.

Ecology is the study of the relation of organisms to their complete environment. The effort to obtain a thorough understanding requires estimates of relative influences and relative values. Values involve theoretical and philosophical conceptions. To the degree that the integration and synthesis of science advances there is a corresponding advance in philosophy. A proper balance is what is needed.

One important practical aspect of an ecological approach is that it may facilitate the integration of the subject matter, and a mutual understanding by scientists and philosophers, as well as the social orientation of both groups.

Ecology occupies a middle ground between the physical, biological, and social sciences, and must deal with human values, as the ultimate tests of value are social, and therefore the theoretical aspects cannot be ignored. Without the social orientation of both science and philosophy, both tend to become perverted to anti-social uses, and scientists and philosophers may waste their lives and lose the freedom necessary for science, philosophy, and a satisfactory society. (Cf. R. S. Lynd, Knowledge for What? The Place of Social Science in American Culture. 1939.)

For an amplification of the value of the scientific method in relation to

social values, see the writer's paper "Selected References on the Relation of Science to Modern Life" (102nd Ann. Rept. of the N. Y. State Museum, State Mus. Bul. 322, pp. 79-96. 1940.)

The American Assocation for the Advancement of Science suggested to the Ecological Society of America, that it organize a Committee on Symposia. Dr. Paul B. Sears is Chairman of the Committee. This is the fourth symposium in this series.

CHARLES C. ADAMS, *Presiding.*

THE RELATION OF PLANT ECOLOGY TO HUMAN WELFARE

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Plant ecology is one of the oldest of the plant sciences. As botany developed as a science, smaller and smaller sectors were selected out and these in turn analyzed. The method of analysis leads endlessly to smaller and smaller sections or subjects. Aided by more accurate instruments, more accurate methods, more careful direction and guidance, the analyst moves into narrower and narrower fields, becomes more and more an authority and less and less capable of seeing the whole or the relation of his subject to the whole.

The ability to see similarities is a matter of synthesis. Synthesis requires broad training and experience and an intellect keen enough to grasp the significance of details without becoming engrossed in them. The holistic approach is inherent in ecology which is concerned with the relation of the plant or community to its environment. Of the endless complexity of the environment the more significant factors must be synthesized to present a general truth. At the present time there is a tendency to try to accomplish this synthesis by the simple trick of organization, by placing in one group men who specialize in all of the various branches; but it is doubtful if the synthesis by organization can exceed the comprehension of the most capable man of the group.

A plant community may be the center of our interest. As such it must be considered in space, in time, in quantity, and quality of its structure, in relation to soil, to climate, to other plants, to animals, and to man. What has happened to determine its character, extent, and composition and what is now taking place and what is likely to take place are all parts of the consideration. But to center attention on the vegetation does not mean that it is the foundation of the structure.

The habitat is made up first of physical space, and the base foundation is rock materials, be they granite, sand, or water. Of this earth material, weather with its temperature and humidity changes and the abrasion by moving water and wind will produce a soil. Soil in a waterless desert or a lightless ocean floor cannot develop a vegetation cover. That can only be produced where temperature, light and humidity are favorable. Vegetation causes modifications in soil and weather conditions but is not the cause of either. This plant cover passes through well-recognized stages of development or

plant successions. On this developing vegetation animals live in the air, in the soil and in the water. This complex of animal, plant, and soil, a living whole, is the base on which man must live. Each of these agencies react on the other, but they are not interchangeable.

The tendency to regard as basic the subject of our thesis, is shown by the geographer who synthesizes the whole into a region; the sociologist into a human community; the animal ecologist into an animal community; the plant ecologist into a plant community; and the metaphysician into the concept of an organism. Each of these investigators approaches the community or region as an organism, at least for purposes of study. That this is important cannot be denied, but it occasionally leads to a failure to tie the community to the earth as a base, the soil and weather as determining factors, and to consider the plant succession and the animal and human interventions which enter in determining the direction of development. Many plant ecologists consider the development of the plant community to a climax as a plant community function which can be accomplished on any soil base. Still, such is impossible until the soil has developed to maturity. Likewise, there is a tendency to regard animal communities as less dependent on vegetation and soil than is actually the case and to speak of balance of nature or complete adjustment when the base of soil and vegetation have not reached such an adjustment.

The term plant community is applied to any grouping of plants and, since it is not defined, it may be applied to a clump of shrubs in the corner of a city lot or to the great band of coniferous timber which circles the earth in northern latitudes. The plant communities have been studied and interrelated in an elaborate system designated by technical terms such as formations, associations, and societies. In studying any one of these it is desirable to recognize criteria for comparison. A very elaborate system could be built up but a simple approach based largely on the historical development of the subject is here presented. Four criteria are used:

1. Physiognomy.
2. Floristic composition.
3. Succession.
4. Response to environment (habitat).

Physiognomy or the general appearance is used as a basis for designating similarity or difference by such descriptive terms as meadow, forest, or brushland.

This was the first criterion used in ecological plant geography. Long before the word ecology was used and before the subject of botany had progressed to anything like a science, during Alexander the Great's expedition through Persia and India in 334-323 B. C. (Bretzel 1903), officers of his general staff described the vegetation of the region and recognized types of

growth similar to those described later by Humboldt. About two thousand years later (1717) Tournefort correlated vegetation with climate and distinguished the difference between the vegetation of the lower slopes and the upper slopes of the mountain Ararat, and a little later (1742) Haller pointed out the zones of vegetation passed through from Berne, Switzerland to the top of the mountain, and in 1768 recognized polar plants, stony sheep pastures, cow pastures, fir forests, birch forests, vineyards and Italian vegetation. Soulavie in 1779-1783 classified climate according to vegetation as orange climate, olive climate, grape climate, castanean climate, and a climate for alpine plants. Great names in this field are Humboldt, 1807 and 1850, who presents a comprehensive view of the physiognomy of plants, and Grisebach (1884) who used the term plant formation and defined it in terms of physiognomy as follows: "I would term a group of plants which bear a definite physiognomic character, such as a meadow, a forest, etc., a phytogeographic formation." But Raunkiaer, 1904-1908, has given physiognomy a technical standing, assuring it a place in the scientific study of vegetation. In reality his was an attempt to show the effect of climate on plants, especially in their adjustment to over-wintering. But it also serves as a physiognomic expression. This elaborate system in its simplified form is about as follows. Plants are grouped in ten classes:

1. Stem—succulents.
2. Epiphytes.
3. Mega and Mesophanerophytes.
   Tropical and temperate evergreen and deciduous forests 8 or more meters in height.
4. Microphanerophytes.
   2 to 8 meters high.
5. Nanophanerophytes.
   Shrubs, etc., less than 2 meters high.
6. Chamaephytes.
   Low brush buds only to 25 cm. above the ground.
7. Hemicryptophytes.
   Dormant buds in upper soil. Above ground parts die away.
8. Geophytes.
   Underground bulbs, etc.
9. Helophytes and Hydrophytes.
   Wet meadow and water plants.
10. Therophytes.
    Plants of favorable season. Short season annuals.

The percentage of the total species which fall in any one class can be compared with the percentage of any other area or a more or less arbitrary standard set up. As usually employed, it is based on the flora, but is

equally applicable to total population or to area occupied by the various classes. This approach would, with suitable adjustments, have many possibilities of application to animal and human communities.

Floristic Composition. This is based on systematic botany; a study of the species, establishment of floral lists, the division of the earth's surface into floristic tracts according to their affinities on the basis of the number of species, genera or families common to them.

Here again the beginnings were far back in botanical history—almost as far back as physiognomy. Tournefort (1717) compared Ararat with other mountains. Other contributors were Linnaeus in 1737, Humboldt in 1805, Wahlenberg in 1812, and DeCandolle in 1855, and in 1884 Drúde listed the floral regions of the world as:

1. Northern,
2. Inner Asia,
3. Mediterranean and Orient,
4. East Asia,
5. Middle North America,
6. Tropical Africa,
7. East African Inlands,
8. Indian,
9. Tropical America,
10. Capeland,
11. Australia,
12. New Zealand,
13. Andes,
14. Antarctic.

This system has also been broken up and the method can be applied to describe and compare any areas or any plant communities.

The technique of approach involves the determination of species; the classification of plants; the compilation of a flora; the division of the earth's surface into floristic tracts; the subdivision of these tracts; and the discussion of the limits of distribution of species, genera, and families. It is concerned with distribution and frequency, endemism, and the relation of flora, of communities and of zones.

Many methods have been proposed:
Field collections and identification,
Lists of species arranged as to
 Abundance,
 Dominance,
 Sociability and
 Constancy,
Distinctive species.

Abundance may be expressed in ten classes ranging from very rare, to very abundant or in five classes ranging from isolated to common, or under any other arrangement of classes.

Quadrats or stations are established and measured by

List quadrats (see Haller, 1870) (Hall, 1870) or

Chart quadrats. (Clements, 1905) or by

Transects to measure zonation or change from place to place.

Succession. Accepting as climax the fully developed community in adjustment to soil, climate and biological factors, succession involves all the changes through which bare or denuded areas pass in arriving at a climax stage.

In the simpler cases the initial invasion as to species may represent the climax as on many desert clay habitats where shadscale *(Atriplex confertifolia)* or salt sage *(Atriplex nuttallii)* represent both the early and final stage. In most cases, however, the stages are many.

Areas successively occupied by different plant communities are passing through different stages of plant succession. This process was also observed long ago, chiefly in connection with peat bogs in the latter part of the seventeenth century. In the early eighteenth century the successions from ponds to forest trees were noted. In this line of historical development many names stand out. DuLue (1806) was probably the first to use the term succession which he applied to the zones about lakes. In our country Peters about 1812 insisted that in agriculture we follow nature's plan of replacing one crop with another and cites many cases where one type of vegetation was replaced by another. Hult (1885-87), Warming (1891-1907) both contributed greatly to the understanding of vegetation change.

In America Cowles (1899-1901) established a school of physiographic ecology and trained a large group of workers in this field. Clements (1904, 1916) has established succession as one of the major criteria for the study of plant communities. He has proposed an elaborate system of technical terms distinguishing the changes from bare rock or sand to climax vegetation, from water to land climax, from disturbed areas to reestablished climax and the changes during geological eras and during the whole period of vegetation occupancy of the earth.[1]

[1] Clements presents the following classification and terminology applied to successions (seres):

- Geosere
  - Eosere
    - Clisere
      - Cosere
        - Sere (climax)
          - Prisere
            - Hydrosere
              - Halosere
              - Oxysere
            - Xerosere
              - Lithosere
              - Psammosere
          - Subsere
            - Hydrosere
            - Xerosere

The methods used in studying succession are the means of migration or the carrying in of seed, spores, or plants by agencies such as water, wind, animals, or man, aided by contrivances such as winged, plumed, hooked, viscid or fleshy seeds, or fruiting bodies, the means by which these plants become established in the new habitat and the adjustments which they are forced to make. It also is concerned with physical barriers such as water, mountain ranges, icefields and deserts, and biological barriers, such as forests, offer to the movement of grassland or desert species.

Usually the well-recognized stages of a succession can be studied as communities and a comparison and arrangement of these communities constitutes an acceptable approach in the study of plant succession.

A knowledge of the natural trends of succession enables the man who manages wild land to work with nature to bring about desired results. Artificial reseeding or planting for soil protection, improving grazing or timber production, for increasing the conditions favorable to man or wildlife should not be undertaken on wild land (land that is not intended to be cultivated or disturbed) without a clear perception of the natural succession on the area. To change this or reverse it means continued expense and in all probability ultimate failure. Often the reestablishment of the natural grass, brush or forest cover is delayed in proportion as a temporary success is secured by the use of the introduced species. Agriculture applied to other than wild land is an intervention intended to stop or turn aside the natural development of the vegetation of the area.

The value of studies in succession is apparent in all practices involving reforestation, reestablishment of grasslands and erosion control by plant cover. Here also enters the biotic phases, effects of competition between plants of the same species, population pressure, competition between species, diseases, and use by animals and man.

It is possible and even probable that a climax vegetation will not be the same where deer graze as where cattle graze, where man herds his sheep and where nature developed bison and antelope or where Mormon crickets, grasshoppers or the plant eaters live. The final adjustment must be effected by the total habitat. Therefore, true climax is probably hypothetical since the habitat is in a continuous process of cyclic change and possibly of a direct drift in one or several directions, and since use by animals is not constant and continuous but varies in intensity and kind. Moreover, too few climax types have been studied in relation to soil development. It is difficult to think of true climax on areas which have not reached at least a somewhat stable state of soil development. Almost every type of grassland appears in various stages of the succession. As an example, the prairie grasses look like climax on deciduous forest podzolic soils, on the deep rich chernozems of central Kansas and on the sand lands of Colorado, the gravel knolls of Montana and the zonal areas around ponds in South Dakota. Only one of these loca-

tions, the chernozem, indicates a balance with a developed soil. The inclusion of all the grasslands of central and western United States in one group, the prairie, does violence to the concept of adjustment to the environment.

Response to Environment (Habitat). Habitat is not a criterion of vegetation at all and should give way to a study of physiological and morphological adjustment which should constitute the fourth criterion. Morphological adjustment such as size of plant, size of leaf, character of the epidermis and leaf structure are associated with physiological adjustments such as low water requirement, decreased transpiration and changes in cell sap density. In this field we still lack an adequate expression of response of the plant to environment. Morphology and physiology should give the answer and methods should be devised to enable one to compare two plant communities as to their response.

Where there is sufficient morphological and physiological information on the individual species their presence or absence in the community may contribute directly to an understanding of the adjustment of the community to the habitat factors.

Response to environment has not played as important a part in plant ecology as one would expect. Advances have been made in the study of the morphology and physiology of the individual plant. The adjustment of the individual plant of the community aids in an understanding of the community. If creosote bush is prominent in the community we know that this community has very marked temperature and moisture limitations. The presence of blue grama instead of side-oats grama indicates a decidedly different water relation than if the latter were dominant. The bacteriologist determines favorable or limiting conditions by the species or strains of bacteria shown as a result of an analysis if he knows the conditions under which the species have always been found, so the ecologist can use the presence or absence of species as indicators of the environment and measure the environment in terms of their known physiological requirements. Many studies deal with such problems as size of plant, spacing, size of leaf, character of epidermis or leaf surface and others with the character of the protoplasm, its hydration and density of cell sap for it is impossible to separate sharply morphological and physiological adjustments.

Attempts to classify vegetation on the basis of adjustments to a single factor, in itself very complex, such as drought, may serve as an illustration. Kearney and Shantz (1912) divided the plants growing in regions subject to drought as:

Drought escaping,
Drought evading,
Drought enduring, and
Drought resisting plants.

Drought escaping. Plants of this group are short season annuals which germinate from seed when moisture and temperature are favorable and quickly complete the vegetative and reproductive growth to produce seeds before the temporary favorable condition changes. They may show little or no ability to stand drought during the growing period or to be economical in the use of water. Most of these plants can produce seed with little growth. Here belong most of the desert annuals, the annual grasses of the southwest and some of the short season field crops.

Drought evading. By limiting the amount of growth and by economical use of water these plants prolong the favorable condition. Here belong the most successful crop plants of the semiarid regions and also many of the native species. Some of the latter are very efficient in the use of water. As a rule, plants of this type are widely spaced, do not grow to large size, are efficient in the use of water and have a relatively high leaf temperature due to a low transpiration rate.

Drought enduring. Plants of this group have the ability to stop growing when moisture is not available and recover quickly when rains come again. Here are the more important desert shrubs and grasses, and most of the semidesert grasses. They may or may not possess drought evading properties. As an example, mesquite does not evade drought any more than does a plant like alfalfa, but it can endure in a leafless stage throughout long periods of drought. Blue grama not only endures drought but is economical in the use of water and therefore helps to evade drought, while side-oats grama is not economical in use of water, but usually in drought country is found where competition is not keen for the small amount of water available. As soon as available water is exhausted, these plants enter a drought rest period which if not too extreme apparently does little or no damage to the plant. Lichens are excellent examples of this type of plant. To some extent, the grape as grown in warmer country belongs to this group.

Drought resisting. Here belong many of the succulent desert plants, fleshy epiphytes and many plants with large underground roots capable of water storage. When water is available it is absorbed and stored, to be used gradually in carrying on the metabolic processes of the plant long after the exterior supply of moisture is exhausted. Many of these plants flower and ripen seeds long after they have ceased to take water from the soil. These plants in addition to drought resistance are usually drought evading plants. They do not produce a large amount of annual growth and are economical in the use of water and often have reduced the plant surface to a minimum. The plant body usually warms up during the day and at night may lose half as much water as was lost during the day. A plant like alfalfa even in a dry climate will lose less than 3 percent at night.

These are adjustments to a drought condition. Similar classifications could be made with respect to cold (frost). There are cold escaping plants,

cold evading plants—where the tops die but the subterranean parts remain alive, and cold enduring plants. One could recognize as cold resisting plants those which can grow at low temperatures such as the arctic salt water algae which grow at very low temperatures, and have adjusted normal processes to a low temperature scale as compared with warm weather plants. Here again these are rather poor examples but some measure will yet be secured which will give us a criterion for measuring the differences in adjustment between a rain forest of the tropics and a spruce fir forest of the north.

Since we have no adequate measure of adjustment to environment we have to fall back on the habitat which is an almost hopeless complex of climatic, soil, and biological factors. Too often the habitat is described but not correlated in any way with the vegetation or even the physiological or morphological studies which follow.

A study of the habitat includes climatic factors, soil factors, and soil development, and demands the most approved methods of physics, chemistry and mathematics. An adequate measure of the habitat involves the measurement of temperature of air and soil at various levels, of light intensity in calories, of air humidity in wet bulb depression or dew point, of evaporation and wind movement, soil moisture and the other physical and chemical characteristics of the soil. Most of these factors vary from hour to hour and day to day and year to year. Complex and difficult as are these measurements, they are meaningless unless correlated with plant response expressed in such physiological processes as transpiration, assimilation, growth, or morphological adjustment, and on the part of the community by changes in physiognomy or floristic composition.

Environment has been defined as including everything external to the community or organism under investigation. Such a definition is useless to the beginning student who must start somewhere and should not begin with a too remote point or with a relatively meaningless factor. A plant community or a plant is not directly effected by all the factors of the environment, at least it is not equally effected by even the most evident factors. Therefore, the important factors are rather definite and often limited in number. It is best to consider adequately a few of the important factors and not try to cover the whole. As an example, plants react to weather, not to climate, which is a generalization.

It is often said that man and animals lessen their dependence on the environment by migrations and seeking shelter. But there is a somewhat similar adjustment of plants. Winter rest periods are more perfect adjustments than the hibernation of animals. The loss of leaves during the winter rest or drought rest periods is as great or greater an adjustment than can be made by man and is only equalled in degree by some of the lower animals.

The habitat is an endless problem. The factors of direct importance are:

Air—Composition,
  Light,
  Heat,
  Humidity, rainfall and
  Air movements.
Soil (or water)
  Physical and chemical character,
  Structure,
  Composition,
  Development,
  Air,
  Moisture,
  Depth,
  Nutrients,
  Biological Complex.
Biological—Plant,
  Animal, and
  Human influences.

Heat is easiest to measure and most difficult to correlate. Thermometer and thermograph records give temperature which if measured in the shade can be summarized. As yet temperature has not been utilized as much as it should be. Possibly the use must await a more detailed study of the physiology of the plant to determine its reaction to different temperature levels. The plant community seems to have definite limitations. However, few have been determined. Many attempts have been made to utilize temperature as a major factor in studying plant and animal distribution, but with only partial success (Merriam, Köppen).

Humidity may be studied by sulphuric acid method or wet bulb method and expressed as temperature at the dew point, relative humidity and saturation deficit, of which relative humidity should be accompanied by temperature and barometric pressure to be significant. Studies of this type are usually made in arid or semiarid countries where their significance is more direct. However, high humidity is likewise a requirement of many important world communities.

Evaporation is usually measured from water surface, from Piche, and from Livingston evaporimeters which cannot be standardized with respect to each other. Evaporation like humidity has been studied most in desert and semidesert regions.

Rainfall may be recorded daily or by means of self recorders. Here again in arid and semiarid regions the variation from place to place is so great that there are generally too few observations to be locally applicable.

Soil moisture. This is a difficult subject. In the laboratory we measure hygroscopic coefficient (Hilgard), moisture holding capacity (Hilgard), moisture equivalent (Briggs and McLean), wilting coefficient (Briggs and Shantz), and unfree water (Boyoucous).

In the field we determine field carrying capacity, wilting coefficient, and minimum point of exhaustion.

No subject is more inadequately handled in ecological work, largely because it is too difficult and too time-consuming to justify adequate treatment. Field determinations under natural vegetation are almost impossible to make. Under cultivated crops it is much simpler.

Movement of moisture in the soil is important when the subsoil is permanently dry as in pedocal soils and when the soil is moist to a water table above which there is a capillary fringe as in the pedalfers. We know more about the former case than the latter.

While we must know something of the physics, chemistry and biology of soils, we must also recognize that soils, like vegetation, pass through successive stages in development leading to a climax condition which is recognized as a mature soil marked out and recognized by a definite profile. Can the animal ecologist be sure that he is dealing with a fully developed animal community if the vegetation is not in a climax stage? Likewise, can the plant ecologist be sure that he is studying a climax in vegetation if the soil is immature? These interrelations demand that for a full appreciation of the contributing factors we must understand the modern phases of soil science, especially those dealing with soil development as indicated in the soil profile, and know something of the great groups of soils.

Radiation. Radiant energy comes from the sun, the sky, and the earth and can be measured in number of gram calories per centimenter per minute. (Humphreys, 1920). The solar output varies from 5 to 10 percent in irregular periods of 5 to 10 days, and in 11 year cycles to the extent of 2 percent. It varies due to changes in the distance from the sun by about 3.3 percent and due to the inclination of the rays, varies from 100 percent at equator to 95 percent at 20°, 79 percent at 40°, 57 percent at 60°, and 41 percent at 90° of latitude, north or south.

Of the total energy, about 37 percent is reflected back at the outer atmosphere, about 63 percent absorbed by the atmosphere and the spectrum band absorption at the surface of the earth shows thousands of irregularities. Most of the earth radiation is absorbed by the atmosphere.

Light has direct effects in furnishing the energy for photosynthesis, prevents etiolation, evaporates water and operates as a length-of-day factor. Indirectly it raises temperatures, increases saturation deficit, causes wind, and dries out the soil. It is measured in many ways:

Radiometer, thermopyle, bolometer, pyrheliometer (Angstrom, Callander, Marvin and Abbott), sunshine recorder, differential telethermograph (Briggs), photo-chemical photometers (Bunsen-Roscoe, Weisner, Clements), photo-electric cells, alcohol evaporation, and black and white porous cups (Livingston), comparison photometer (Wagner, Sharpe-

Millan, Kimball), spectroscopic measurements (Zederbauer), spectro-photographs, spectro-photometer (Langley bolometer).

In many of these fields new instruments are being rapidly perfected. The duration of light is found profoundly to influence flowering and fruiting period in plants as well as the activities of animals. Such influences are probably at work in determining north and south limits of growth of many plants.

Attempts such as those of Merriam and Köppen to use temperatures to determine distribution of plants or animals are only partially successful. Similar attempts based on humidity are also only partially successful. The utilization of the two has of necessity required arbitrary adjustments. Too little is known of the plant physiology of a sufficient number of the plants which make up the plant cover to enable one to evaluate either temperature or humidity or both in relation to the community considered.

While transpiration can be correlated rather closely with depression of the wet bulb and radiation in calories, it does not follow that growth would be correlated with transpiration. Most of the attempts so far made have not been based on physiology but on a plan of dividing earth surfaces up on the bases of temperature and humidity or both and trying to fit in known distribution of plants or animals with this pattern.

The habitat is endlessly complex, and to synthesize the many factors into a whole seems all but impossible. This is one of the reasons why the community has been used as an indicator. As an example, tropical rain forest indicates high temperature and high humidity, with no cold or drought rest periods. Sagebrush is found only in temperate desert country, on a non-saline soil, with both drought and cold rest periods.

Usually the formation groups conform in physiognomy and habitat. They can be broken up on the basis of botanical composition and succession. Smaller and smaller communities are correlated more closely with detailed differences in habitat. In any given climate, soil differences are correlated usually with vegetation changes, indicating the physiological differences shown by different species. However, on the basis of broad groups as an example, deciduous forests are found on all types of soil if measured in terms of earth material. The correlation with soil profile is much more real and indicative.

Attempts to synthesize climate or other habitat factors are accompanied with great difficulty and can only be useful when they can be correlated with plant communities. Judging land on the basis of natural production, or production under cultivation where plants are grown would seem to be on a better basis if plant communities are used than any synthesis of the complex environment yet presented.

Vegetation of the earth and its relation to man's use. If the great physiographic divisions of the earth's surface are exempted, the surface is marked more distinctly by vegetation cover than by any other feature. Primitive man recognized the plant cover not only as a source of sustenance and pro-

tection but likewise as a guide in his hunting and in his choice of the best locations for the cultivation of his food crops.

The earth's vegetation may be classified into great formation groups, each producing not only native plant products valuable to primitive and civilized man alike but also supporting an animal population of value and indicating climatic and soil conditions favorable to cultivated crops.

As a synthesis of the environmental factors the plant community excells the individual plant since it is in itself a synthesis of the many species with their varying morphological and physiological adjustments. It has had time to come to at least a partial adjustment to the habitat factors.

Large communities such as the tropical rain forest (a formation group) and the deciduous forest (a formation group) have considerable uniformity of physiognomy, succession and response to environment but may differ distinctly in floristic composition. Formations have more floristic uniformity while the smaller and smaller divisions, associations and societies, etc., have greater and greater uniformity in physiognomy, floristic composition, successional stages and response to environment. The two groups here mentioned are roughly alike in physiognomy since they can both be included in the designation forest, but they are quite distinct with respect to succession, floristic composition and response to environment. Their habitat is distinctly different.

Broadly, the earth vegetation is classified on a physiognomic basis as

Forest,
Grassland,
Desert,
Water surface. (Figs. 1 to 4.)

A few of the more important formation groups may be mentioned as examples.

Tropical rain forests circle the globe on land areas in the tropics. These are luxuriant evergreen forests with no drought or cold rest period, characterized by a great mixture of species of trees of unequal size and age. The canopy is dense and in places entirely shuts out the undergrowth. It is a many-storied forest or, as Humboldt said, "A forest piled upon a forest." As a rule, the evergreen leaves are thick and leathery. The bark of the trees is thin and the flowers relatively few and may be found either on the top of the canopy as in the Cynometra forests of the Congo or on the main stems and thick branches as in trees such as the figs. This forest indicates quite definitely a tropical soil with a tendency to be lateritic, a warm damp climate throughout the year and a rainfall of 60 inches or more distributed throughout the year. There is no drought or cold rest period. This plant community is the home of a rich fauna, many of the forms being confined almost entirely to the tree tops, such as birds, squirrels, baboons and monkeys. Large mammals such as okapi, buffalo, elephant, warthog, and along rivers

the tapir, hippopotamus and crocodiles make up only a part of a rather rich fauna.

Primitive man has lived largely on native products. Where agriculture has been developed the forest was totally or partially destroyed and crops planted along rivers or in openings. Oils, rubber, fruits, nuts, and fibers are collected. Tropical fruits, vegetables, grains and root crops and staple food crops such as corn, rice, cassava, banana and many others are grown.

Civilized man has used this tropical rain forest belt for crops of great importance to him. Cacao, rubber, sugar cane, vanilla, ginger, rice, cassava, coconut and many tropical timbers, gums, oils and fruits are brought to his home in the temperate zone from this great forest belt. This forest occupies less than four million square miles of the earth's surface, chiefly in Africa, South and Central America, southeastern Asia, the East Indies and north Australia.

The deciduous forests of the northern hemisphere occupy three great areas: the eastern part of the United States, western Europe and eastern Asia. There are two distinct physiognomic phases. During the growth period it is characterized by a dense foliage, the leaves, almost grass-green tin color, becoming yellow or reddish in the fall. Later the leaves fall, to leave bare branches well protected by heavy bark and the buds by scale leaves. This condition prevails throughout the cold rest period. The physiognomy is similar, the adjustment to environment similar, but the floristic composition is different on the different continents. Still, even in composition there is a similarity in that in America oak is most important with maple, birch and hemlock, in Europe, birch and oak and in Asia, ash and birch.

The soils are the grey-brown podzolic soils, and in the north the lighter less-developed numbers of this group. Various members of the deer family, bear and many small animals and birds constituted a rich fauna in these areas.

This forest has produced much of the timber and fuel used by civilized man during the expansion period. Much of the timber was wasted in clearing to make room for crops. Two generations ago these were the most important agricultural lands of the world, used for the production of temperate cereals, fruits and vegetables, and hay and pasturage. This has been the region on which our race largely depended for vegetables and animal foods, timber and fuel until the grasslands were settled and improved transportation made coal available as fuel.

This area occupies about six and a half million square miles of the earth's surface.

Tall Grass. The prairies of North America, the pampas of South America, the high veldt of South Africa and portions of the steppes of Russia are pure grasslands. While grasses predominate and for the most part grasses of the andropogon group, there is a wealth of flowering herbs which at times, especially in early spring, often color the landscape. In the fall the

grasses mature and the dry season is conducive to fire which often sweeps over the area. There is a drought and a cold rest period and growth begins when spring temperatures rise above the growth minimum temperature. On most of these areas fire has been a natural factor, set by lightning and often used by the nomadic primitive peoples to aid in hunting or to improve the accessibility of green grass in spring. The soils are among the deepest of the pedocals and in places such as North America may verge on pedalfers along the moist eastern boundary. At the dryer western edges they are tropical chernozems. All are rich soils more productive by far than those on which our race relied when using the podzolic soils of the deciduous forest areas.

These grasslands were occupied by nomadic tribes and not entered by civilized man until he had rather fully occupied the deciduous forest area.

Productive under cultivation beyond any soils previously occupied, if we except rich alluvial river bottoms, these have become the granaries of the world, and have been almost entirely reduced to cultivation. In the south or warmer portion they produce cotton and warm-weather cereals.

Civilized man now relies largely on these lands for his grains and much of his feed for domestic animals. A little over one and a half million square miles of this type of land is found on the earth's surface.

Desertgrass savanna. This is a carpet of shortgrasses or open bunchy grasses with small trees scattered through evenly or in clumps. The trees seldom exceed ten feet in height. It is found in the hot dry tropical and subtropical zone.

In the United States, mesquite, ziziphus and cacti are scattered over a grama, buffalo or mesquite grass cover, in Australia, dwarf acacia, casuarina and eucalyptus, over a grass cover of Mitchell and other grasses, while in Africa, acacia, ziziphus, combretum and terminalia cover a grassland of aristida and schmidtia.

Rainfall is low and drought periods 5 to 8 months long; most of the plants are drought enduring. In Africa this type is characterized by a fauna rich in both species and numbers and the great concentrations of big game are mostly in this type. It is excellent grazing land of low carrying capacity. Herbivora and the accompanying carnivora and scavengers are abundant, and primitive men as well as Europeans have used this land for their domestic herds. Only under the most favorable conditions is agriculture attempted without irrigation. It is an ideal country for the use of a nomadic pastoral people for all or a part of the year.

Two and a half million square miles of the earth's surface is characterized by this type.

These examples must suffice to show that areas can be marked out by the plant community which have definite characteristics directly correlated with the productivity of land either in a wild state or under cultivation. It

is on this base that man must subsist and which must be an important consideration in any study of human ecology. Human ecology must go beyond but up to a certain point it is inseparably tied to the land and the plant cover.

Man must either use land in a wild state or modify it to produce cultivated crops.

Wild land always has been and will continue to be important to man. Of the world area, fully half of the land has a climate unsatisfactory for production of cultivated crops; and only a small percentage of this semidesert land can be used by irrigation.

In the United States a little more than half of the area has a favorable climate. Of the half which lies under a suitable climate, much of it is unsuitable for crop production because of unfavorable soil or topograph. In the United States about one half of our land is in farms and one half of the land in farms not cultivated. It seems probable that on a world basis wild lands will always greatly exceed cultivated lands.

It may not be stretching the point too far to say that wild land has been and will probably continue to be the back-log of civilization.

In the management of wild land, plant succession as influenced by use by wild or domestic animals becomes of major importance. Only a thorough understanding of the indicators of change either of improvement or deterioration can serve as a guide to management practices.

As the relative importance of wild and cultivated land comes more into the plans of civilized man, the ecological approach will become increasingly important. Up to this time no thought has been given to retaining a back-log of wild land as such. We have conserved forests but not necessarily wild land. Our philosophy has been to bring under the plow any available areas thinking that by so doing we were increasing man's dominion over nature. Now the proper use of wild land becomes a major consideration. Waste in any form is abhorrent and use of wild land for man's needs and comforts is inevitable. Such use clearly raises many ecological problems, since the correct path between waste on one hand and abuse on the other is one requiring the consideration of the many problems of the environment and man's ecological needs.

In all probability use of wild land for wildlife, domestic herds or timber or wild hay will often involve its use in a successional stage below the true climax. As an example, in the Northwest, Douglas-fir forests are more desirable than cedar and hemlock which would replace the former and which require too long a time to reestablish themselves. It is also probable that grazing land may be so managed as to remain the better browse species which might be replaced if given total protection.

Man is dependent on raw materials on which to live and build his industries and institutions. Of the raw materials of the world, over two thirds are directly of plant origin as food, fiber, wood, oils and gums; about two

thirds of the remainder are of animal origin such as meat, butter, milk, skins, hides, wool, furs and fish products, all of which are derived from plant directly or indirectly. Of the remaining portion about nine tenths are in the form of coal, gas, and oil also directly or indirectly derived from plants, and only a few percent come from other than the plant sources. This is only another way of saying that for food and energy we are dependent on the sun and that the green plant is the machine which catches this energy and converts it into usable materials and food for the use of animals and man.

The most important evaluation of climate, or of soil, is that measured in its relation to plant production. The plant community indicates more clearly than any series of factor measurements the climatic conditions, the soil conditions and the biological impingements which have shaped it as to physiognomy, floristic composition, stage of succession and morphological and physiological adjustments of its unit organisms. On this plant community, and often as an integrated part of it, the animal population lives. Man utilizes this plant and animal community directly or indirectly as a base on which to build his industries and his cultures.

The application of plant ecological methods to human ecology can best be made by the human ecologist or by the two working together. Naturally each is least at home in the other field which in each case has become somewhat technical.

The criteria here used in plant ecology could be used in animal and human ecology. Most important in any case is a consideration of the land and by such a term is usually implied land clothed with vegetation, which holds it in place and enriches it by the addition of organic matter.

Approaching the subject of human ecology from a plant ecologist's point of view, the writer would be tempted to use first a broad grouping such as forests, grasslands, and deserts in recognizing in man such groups as predator, hunting, pastoral, agricultural, and industrial groups; such floristic types as pine, oak and sagebrush with racial makeup of the human community, including its physical, economic, social, political, and religious background. With plant succession the trends of development are by migration and differential reproductive rate of communities, towns, races, or nations. In reaction to environment the human ecologists have probably gone further than the plant ecologists. But both lack definition in measuring adjustment to environment. Environment affects culture as is shown strikingly in dry countries where Hopi and Kaffir hold rain dances which are not expected or found among Eskimos or Iroquois. Even in the United States we expect Finns in the north and Spaniards in the southwest. Still, as in the plant ecology, we still lack a measurement of the response of man physically, physiologically, socially and economically to changed environment.

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FIG. 1. *(Forest.)* A dense growth of large evergreens with the forest floor well covered with ferns and shrubs. Redwood Forest, California. Figures 1-4 illustrate the great divisions of earth vegetation.

FIG. 2. *(Grassland.)* An uninterrupted expanse of grass with a rich admixture of herbaceous plants. Bunchgrass in eastern Colorado.

FIG. 3. *(Desert.)* An expanse of sand which only after rains produces a crop of short season annuals. Sand desert, Anglo-Egyptian Sudan.

FIG. 4. *(Water Surface.)* The water surface of the earth is occupied with a rich flora of plankton and near the shores benthos develops. Here the large brown seaweeds show on the surface. Near Capetown, South Africa.

Fig. 5. A luxuriant vegetation of vines, bananas, and trees similar to Fig. 6 in luxuriance and appearance but differing in having no plants in common. Temperate Rain Forest, Kenya Colony, Africa.

FIG. 6. A luxuriant growth of ferns, shrubs, and spruce, similar to Fig. 5 in luxuriance but with no species in common. This vegetation can resist cold but has no ability to withstand drought. Sitka Spruce Forest, Alaska.

FIG. 7. This vegetation resembles closely that in Fig. 8 in appearance and conditions of the environment. It is adjusted to avoid and endure drought and withstand a long cold rest period. Grama grass, Stipa and Artemisia frigida, Montana.

FIG. 8. Similar to Fig. 7 in appearance and conditions of the environment. It is also adjusted to avoid and endure drought and withstand long, cold periods. Festuca, Stipa, and *Artemisia meritima*, Lake Elton, Russia.

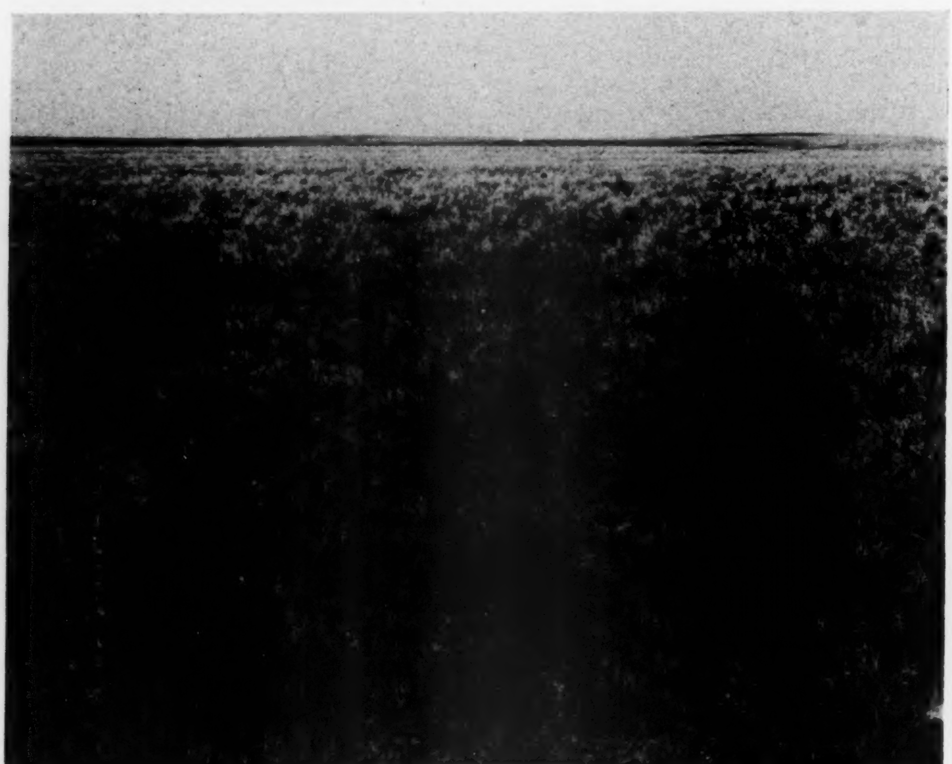

FIG. 9. Wiregrass vegetation on undisturbed land where the soil is sandy. Eastern Colorado.

FIG. 10. Shortgrass on the right. At the left plowed and abandoned for about 12 years. The wiregrass vegetation here is identical with that on undisturbed sandy land shown in Fig. 9. Eastern Colorado.

FIG. 11. Badlands show as many as five levels of stabilization. The shortgrass reestablished on each succeeding level, except the lowest, has reached a climax stage since no differences can be detected. The soil may show differences on analysis but they are not evident on casual examination. Badlands, South Dakota.

FIG. 12. A profile from Fig. 11 showing blue grama and a typical fully developed soil profile. Badlands, South Dakota.

FIG. 13. A stand of mature Douglas-fir with cedar and hemlock coming in as an understory. In a thousand years or so they will replace Douglas fir. Washington.

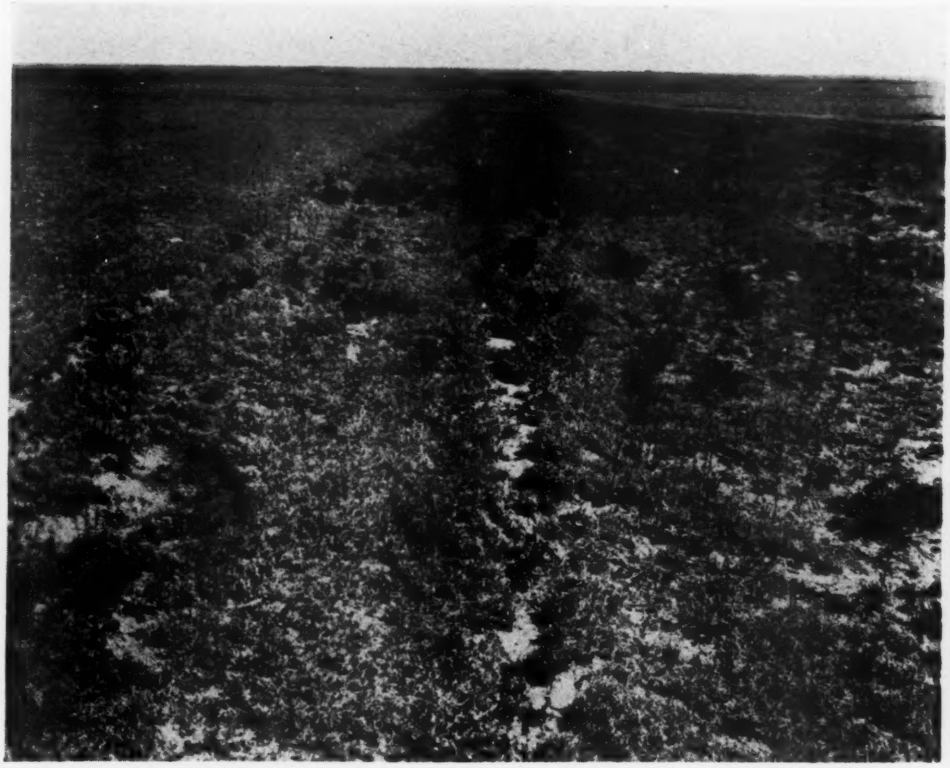

FIG. 14. Shortgrass destroyed by roadways has reestablished itself in the road at the left after about 25 years. At the right on roads abandoned for a shorter time matchweed and Schedonnardus stages are found. Abandoned roadway, eastern Colorado.

FIG. 15. Sharp differences in vegetation from open water in the right foreground to floating vegetation farther back; reeds and rushes, willows and aspen in the back. These are stages in development in which the water or soil changes precede the vegetation changes. Alberta, Canada.

FIG. 16. A sharp demarcation between Kochia vegetation on fine saline soil at the left and sagebrush on porous non-saline soil at the right. A change in soil would bring about a change in vegetation. Tooele, Utah.

FIG. 17. Drought is evaded partly by wide spacing in deserts. Here plants are far apart and can draw on a large mass of soil for moisture. Vegetation is more dense along drainage channels. Growler Valley, Arizona.

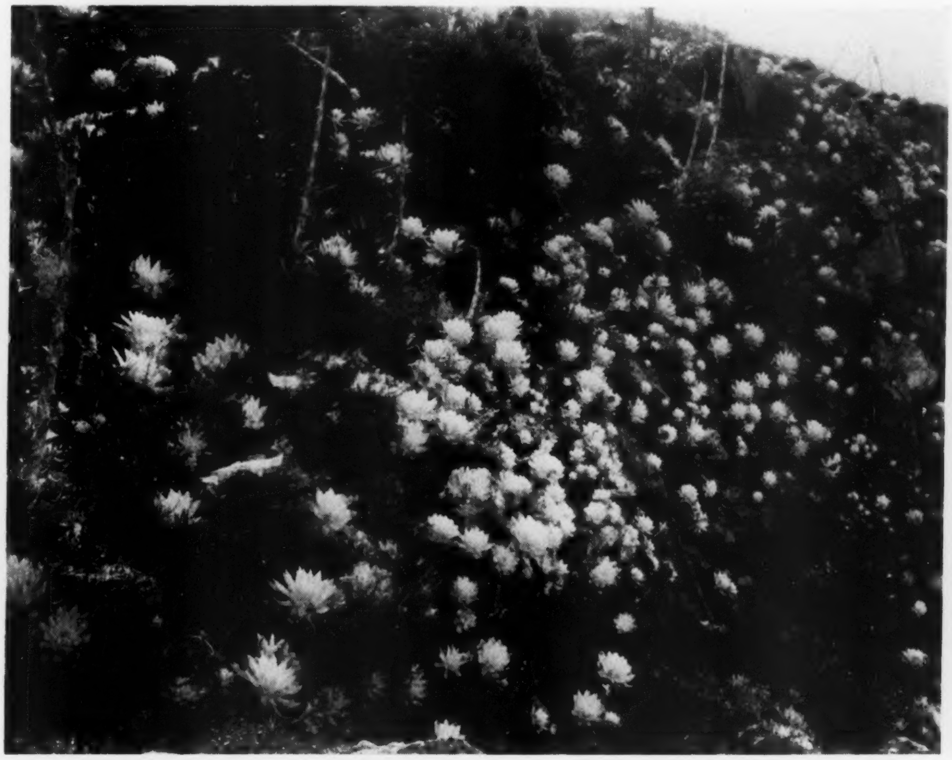

FIG. 18. A dense growth of desert plants some of which are drought evading and drought resistant, but there is no wide spacing. Compare with Fig. 17 as to density. Mostly Agave and Dudleya. Encinada, Mexico.

FIG. 19. Drought escaping plants such as the California poppy, drought enduring shrubs and drought resisting cacti. A dense mixture with little opportunity to evade drought by wide spacing. Picachio Peak, Arizona.

Fig. 20. Drought evading by wide spacing in almost pure stand of *Hillaria rigida*. Yuma, Arizona.

Fig. 21. Drought enduring shrubs, grasses, and trees. The thin stand contributes to drought evasion. Droughts are from 5 to 8 months long. Oaso Nyiro, Kenya Colony, Africa.

FIG. 22. Drought resisting cacti which absorb water when the soil is moist and store it for use during periods when no water can be obtained from the soil. Sahuaro Forest, Tucson, Arizona.

Photo by U. S. Forest Service

FIG. 23. Vegetation browsed by deer. Juniper is trimmed as high as deer can reach (6 feet). Had this area been used by sheep these grasses and shrubs would have been eaten but the juniper not taken. Kaibab, Arizona.

FIG. 24. Vegetation is browsed by elk to about 9 feet. They have a tendency to break the branches down. Deer seldom do this. Elk also use more of the ground cover.

FIG. 25. Sheep, if concentrated, eat almost everything in reach. They seldom eat juniper and this photo should be compared with Fig. 23. When properly herded and controlled as to number the range can be used by sheep without noticeable damage to the vegetation. John Day, Oregon.

THE RELATION OF GEOGRAPHY TO HUMAN ECOLOGY

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This is no place to undertake a discussion of the controversial question of "What is geography?" Nor shall I consider the merits of the familiar definition that "Geography is human ecology." There is a popular understanding that geography deals with areas or with the areal differentiation of the earth. There is likewise a popular understanding that human ecology, by analogy with plant ecology, deals with the development of the human community and its mutual interaction with the totality of the environment.

It would seem that human ecology must transcend all of the present academic disciplines, and that the development of a science of human ecology must involve cooperation of geography, sociology, demography, anthropology, social psychology, economics, and many of the natural sciences as well. Progress in human ecology requires a certain reorientation of the existing disciplines to emphasize the ecologic concept, which has been so admirably developed and presented by the botanists.

In the brief time at my disposal I can do little more than give an illustration of the sort of contribution which geography can make to the science of human ecology and because of my present interest in soil conservation, I have selected one from that field of activity.

Since the beginning of the earth's history two great opposing sets of elemental forces have been at work moulding and sculpturing the earth's surface. Internal stresses have resulted in the uplift of broad portions of the earth's crust and the upheaval of mountain masses. At the same time, external forces have been active in leveling the irregularities in surface produced by such upheavals. These are the relief-creating and the relief-destroying forces. The first, man is powerless to alter in any respect; but the second he has, perhaps unwittingly, modified to such an extent that they may eventually destroy him.

At first, in the absence of water, the leveling process must have consisted exclusively of slides and avalanches of rock and debris which had been separated from the parent rock mass by alternate heating and cooling. The earth, devoid of all life, had no protective cover of vegetation and if viewed from the height to which the stratosphere balloon ascended a few years ago, its surface would have appeared like that of the moon as it will be seen through the new 200-inch telescope now being erected in the West. Moun-

tains were much higher, basins were deeper, and major slopes were steeper than at present.

The first vapors condensing and falling to the earth as rain initiated a new process of land sculpture. As the water flowed down the slopes and began to collect in the depressions, some of its energy was employed to transport the products of rock disintegration. Running water is a powerful instrument of erosion and with the initiation of the water cycle, consisting of evaporation, condensation, precipitation, and run-off, a new equilibrium between the relief-creating and the relief-destroying forces was established. Transport of material was much accelerated and mountains were lowered and slopes reduced in steepness.

As water accumulated in the basins, and the earth's surface became differentiated into oceans and continents, there developed sharp regional variations in climate. Some parts of the land surface received much rain, other parts little or none, and the intensity of the rainfall also varied from place to place. Consequently, there was considerable variation in the rate of erosion and thus in the appearance of the landscape. Even though the earth was still devoid of life and without a cover of vegetation, rainy and dry regions and the various intermediate types of climate could have been identified by peculiarities of surface brought about by variations in the form and intensity of erosion.

Thereafter, in the coastal waters, primitive forms of plant life developed, and gradually organic differentiation produced special types of plants adapted to nearly all of the various types of environment. Eventually, practically the entire land surface of the earth was clothed with a protective cover of vegetation.

The degree of protection provided against erosion varied with the type of vegetation. In the arid climates there was insufficient moisture to permit the development of a plant cover capable of reducing erosion by any considerable amount. In the subhumid and humid climates the grassland and forest vegetation offered almost complete protection.

Thus, as the earth became clothed, the processes of erosion and sedimentation were profoundly modified. For the first time soils could develop. Soil is much more than decomposed rock. It is made up of mineral substances from rock but it also contains organic matter, micro-organisms, and water. The development of a soil involves the upward and downward movement of water, which brings about a sorting of the mineral and organic particles and tends to concentrate the finer clay materials, and in certain soils organic matter, some distance beneath the surface and leave the coarser sandy materials at the surface. The soil-forming process requires water and vegetation, but in addition, time.

The protection afforded by the plant cover greatly reduced the rate of removal of the surface and allowed time for the soil-forming processes to

work to completion. Variations in intensity and amount of rainfall and in temperature regime and the resulting variations in plant cover from place to place combined to produce regional variations in the mature soils.

The chief effect of the development of a vegetation cover and a mature soil on the processes of erosion was a sharp reduction in the amount of surface run-off. The loose, sandy topsoil, high in organic content, absorbed a large proportion of the rainfall. Furthermore, much more moisture was returned directly to the air by transpiration from plants than could have been returned by direct evaporation from the land surface. The roots and stems of plants and the plant litter also retarded the surface flow of water. Thus, for several reasons, surface run-off and floods were reduced after the diffusion of vegetation over the earth; and surface removal of soil through sheet wash must have been very slow and gullying almost completely prevented.

There was a profound difference between the destructive processes in humid and in arid lands. In the humid and subhumid areas the surface was completely covered with vegetation and with the organic products of plant life. The dense root mat in the grassland and the leaf-mold and litter on the forest floor gave almost, if not entirely, complete protection from the action of running water. In arid climates where there was no such dense cover of plant material, protection from the effects of running water was not afforded and gullying and sheet wash, as well as wind erosion, were all naturally active.

Only day before yesterday, as geologic time is reckoned, a new geologic agent emerged upon the earth. This agent was man with his culture. Man has selected a few plants and a few animals from among the many and through the course of his history has developed more and more effective means of assisting them in the struggle for existence. Just as in Ohio and Indiana the oak-hickory and beech-maple forests were displaced by corn and wheat, similar displacements were effected over most of the globe.

The ecology of man's agriculture is profoundly different from the ecology developed by nature through the ages. Nature has brought together associations of plants which live together in general harmony, often aiding each other in various ways, and always contriving to preserve a cover over the soil throughout the year. Man, on the other hand, has produced an ecology in which for a time almost every year the vegetation cover is completely removed and the ground is as bare as in the ages before the advent of plants. Man's concentration on a single plant means, too, that except for weeds which he diligently destroys there is a ground cover only during the growth period of the crop, which is ordinarily not more than a third of the year. Most of the plants which have been selected for crop production are such that, except for man's intervention, they would be unable to survive in competition with other plants. This intervention is what we call agriculture. Agricultural

practices consist of ingenious methods for turning the ecologic balance in favor of the selected group of plants and against all others. Under many of these methods, erosion is greatly accelerated, and may be even greater than in the ages before life had appeared on the earth. It is this accelerated erosion that is known as soil erosion.

The immediate effect of clearing and cultivation of the land and the destruction of the protective cover of vegetation in humid climates is to introduce the erosion processes characteristic of arid lands and to develop, on a small scale, forms which resemble those normal to arid climates. The gullies in the southeastern part of the United States introduce sharp angles and steep straight slopes into a surface where they were originally lacking.

The destruction of the vegetation cover and the beginning of cultivation do not merely introduce arid erosion into the region, however. Lack of protection against erosion becomes the same in humid and arid regions. But precipitation intensities and amounts are both much greater in humid than in arid climates. Thus, the erosion introduced into humid lands is not only different from that originally present but is also different from and much more serious than that normal to arid regions.

Thus, there have been four erosion periods. The first period occurred during the earth's childhood and in the absence of water consisted solely of gravitational movements of rock fragments fractured from the parent body by temperature changes. The second period involved the work of running water before the earth's surface was clothed with a protective mantle of vegetation. The form which erosion took in any region depended entirely on the resistance of the rock, the steepness of the slopes, the intensity and amount of rainfall, and the temperature regime. In the third period these factors were still important, but they were strongly modified by the presence of a vegetation cover and a soil mantle, which greatly reduced the rate of erosion and altered its form. The fourth and present period is the one which, with the destruction of the vegetation cover, marked the initiation of soil erosion. As the soil is removed the factors of rock type, slope, rainfall, and temperature are regaining much of their original importance. It is too often overlooked that soil is more than mere dirt, that it is the end product of a long series of developmental processes which proceed much more slowly than the present processes of destruction. It is not likely that soil science will be able to devise means of speeding the process of regeneration to any appreciable degree.

Erosion is a geologic or physiographic process, the character of which depends upon soil moisture and surface run-off relations. These in turn depend in part on climate and in part on the type and density of plant cover and the structure and profile of the soil. Both plant cover and soil are disturbed and modified by land use. Thus, the circle of dependence of climate, surface, slope, soil, vegetation, and human land use is complete.

These phenomena comprise the subject matter of geography, plant ecology, and human ecology; the difference in these disciplines being not a difference in content but rather of objective and approach. At the risk of being academic, and in spite of the fact that this is probably not an appropriate place for a discussion of definitions, I submit my views as to the way in which these three disciplines may share the same subject matter. Geography, being concerned with the areal differentiation of the earth, deals with regions as botanists deal with plants or zoologists with animals. Climate, surface, slope, soil, vegetation, and land use are elements of the region. The variation of these and other elements and their arrangement in space produce the world pattern of regions.

The development of plant communities and the mutual interrelations of these communities with all of the other elements of the region are the concern of plant ecology. Plant ecology is not a subdivision of botany but is a synthetic science consisting of parts of botany, climatology, pedology, physiography, agronomy, and doubtless other fields of study. Great further progress in plant ecology need not be expected until botanists recognize the need for cooperation and relinquish their virtual monopoly of the subject.

Similarly, the development of human communities and the interrelations of these communities with the totality of the environment is the concern of human ecology. Human ecology can no more be a subdivision of sociology or anthropology than plant ecology can be a subdivision of botany. This fascinating new field can develop freely only as a cooperative enterprise.

Geographers, in considering the multitude of elements whose variations account for the diversity of regions on the earth's surface, must deal with both physical and cultural phenomena. Geography is a science involving a high order of integration, using as it does the findings of geology, climatology, pedology, geomorphology, and many other natural and social sciences. Human ecology similarly involves integration, but presumably on a still higher plane since it embraces other social sciences, the subject matter of which has never been claimed by even the most aggressive and ambitious of the geographers.

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REGIONAL PLANNING AND ECOLOGY

By

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This title implies a discussion of the relation of regional planning to ecology, and of the problems going with such relation.

Discussion of the relation itself would seem to be a fairly simple matter; it amounts apparently to a few clarifying definitions. What is *ecology,* and what is *regional planning?* But these are big questions in themselves. They are questions not of fact nor principle but of mutual understanding. Toward this a start can be made through the dictionary and the encyclopedia.

Ecology is defined as the relation of organisms to their environment. Human ecology, then, would be the relation of human organisms to their environment. And from this it would seem to follow that human ecology, when *applied* to the actual needs and welfare of human organisms, is the search for the *optimum* relation to environment.

Environment is "the sum of the agencies and influences which affect an organism from without; (extrinsic conditioning as opposed to intrinsic)."

Regional planning is best defined by splitting the term in two. What is *planning?*—and what is *region?* These terms for the purposes at hand, are still in the making. They involve not merely what the dictionary states but what it is that planners really mean.

The term *planning* appears to cover two basic ideas: (1) contriving and (2) recording. Which does the planner have in mind?

Let us take the case of the civil engineer in "planning" an efficient railroad grade across a mountain range. His first job is to record or map the topography, and thus to visualize the environment in question. Somewhere in this there exists already some particular line across the mountain range, which marks a grade more efficient than any other line across said range. The engineer proceeds to *find* that line already fixed by nature; he does *not contrive* or invent some line to suit his fancy. Thus the engineer visualizes the potential railroad grade there already within the actual terrain.

From this case we should say that planning is *discovery* and not invention. It is a new type of exploration. Its essence is visualization—a charting of the potential now existing in the actual.

And what is the thing that is planned? Is it an *area* or a *line* merely, or is it something else? It is something else. The engineer plans for something more than a line across the mountain; he plans for *movement* of freight and passengers. And so with planning generally: the final thing planned is not mere area or land, but movement or activity.

This truism gives a clue to what the planner means by *region*. It is something more than area, it is an area or seat of movement; it is what the dictionary calls a *sphere* ("a circuit or range of action or influence").

A good example of a "sphere" is the "range of action" of water within a single river system. Take the Ohio River system. The flow of water at Cairo is influenced by that at Pittsburgh and in the Allegheny headwaters; it is influenced by the flow from the entire Ohio River watershed. If we would plan the flow of a river the object of our planning would be the watershed; this would be the "region" to be planned; *not* as an *area of land* but as a *range of water flow*.

Another example of sphere or region is the range of action or flow of some *commodity* (such as milk) with respect to some city such as Columbus. This city (and every other) is the center of a "milkshed" bounded by a "divide" nearly as definite as that of water drainage. Milksheds (and "commodity-sheds" generally) differ from watersheds in that they overlap. But each one is a sphere of unit flow or movement, and hence a "region" in the planner's sense.

A third example is the range of flow of *population* with respect to the city of Columbus. This city (and every other) is the eye of centrifugal flow as well as centripetal. A tendency exists of population movement from center to outskirts—what is called the "backflow" into the suburbs and beyond along the radiating highways. Here again we have a series of overlapping spheres or regions.

These three examples illustrate the respective ranges (or regions) for the three kinds of movement (or flow) with which the regional planner is concerned: they are (1) water flow; (2) commodity flow; and (3) population flow.

* * * *

We are now prepared to suggest a definition of *regional planning*. But let us first turn to an encyclopedia:

> Regional Planning, a term used by community planners, engineers, and geographers to describe a comprehensive ordering of the natural resources of a community, its material equipment and its population for the purpose of laying a sound physical basis for the "good life". . . . Regional planning involves the development of cities and countrysides, of industries and natural resources, as part of the regional whole.
>
> Encyclopaedia Britannica, 14th Edition, 1929.

Being the co-author with Mr. Lewis Mumford of this definition of the Britannica article, I feel at liberty to interpret it. The elements contained follow:

1. "A comprehensive ordering." This refers to a visualization of nature's permanent comprehensive "ordering" as distinguished from the interim makeshift orderings of man. In this we would apply the thought of Plato—"To command nature we must first obey her."

2. An ordering of "development"—a development of "natural resources," of "material equipment," of "population," of "cities and countrysides," of "industries." Such development implies movement, activity, flow—comprised in the three flows mentioned of water, of commodities, and of population.

3. "A regional whole"—which implies an integral or unit sphere of activity, or range of flow.

4. The purpose of the "good life" (or optimum human living—what Congress calls the "general welfare," Jefferson's "pursuit of happiness").

We may now restate the Britannica definition in more specific terms:

> *Regional planning* is a comprehensive ordering or visualization of the possible or potential movement, activity, or flow (from sources onward) of waters, commodities, or population, within a defined area or sphere, for the purpose of laying therein the physical basis for the "good life" or optimum human living.

The relation to ecology of general planning as here defined is, as stated, a simple matter indeed. Regional planning is ecology. It is *human ecology;* its concern is the relation of the human organism to its environment. The region is the unit of environment. Planning is the charting of activity therein affecting the good of the human organism; its object is the application or putting into practice of the optimum relation between the human and the region. Regional planning in short is applied human ecology.

* * * *

So much for definitions—the attempt to understand the key words that we use (ecology, region, planning). So much to make sure that we know indeed "what we are talking about." . . . And now what of it? Of what earthly use (or human use) is human ecology? Answer—none at all except as it is applied. Here then our subject really begins. How to apply our definitions and the tenets they imply? How to adapt environment to folks, and folks to environment? How to do it for the purpose of optimum living for the folks?

Let us cite one illustration. Take a particular environment such as the region or sphere of water flow in the Ohio River system. How to adapt this sphere (this particular environment) to the inhabitants thereof? This is a problem in charting water flow. And *vice versa:* how to adapt inhabitants to habitat? This is a problem in charting population flow.

Here is a mutual charting—of region to man, and of man to region. There is nothing new about this mutual regional planning—it is as old as man himself. Yet we are just beginning to tackle it in a comprehensive would-be-scientific manner.

What are the elements of this mutual—this twin—this complemental—problem? These elements focus largely in the river flood plain. How should this plain be divided between river and man? What is the natural zone of water flow—high water as well as low? What is the legitimate zone of

human occupancy—whether for work or general living? What portions of the flood plain belong respectively to river—and to man?

The river's portion, within limits, can be modified by man. He can restrict the river in one place by expanding it elsewhere. He can narrow the river's precinct in the flood plain downstream by storing the river's water on the flood plain upstream. Thereby he widens man's domain downstream by restricting it upstream. He pays his money and he takes his choice.

What should this choice be? What is the proper balance of man's flood plain domain as between upstream and downstream? How much flooding is warranted of rural valleys on the Ohio River tributaries to prevent flooding of urban centers on the main Ohio River? Not but what the Ohio flood plain between cities can be used for farming and various purposes, even though occasionally flooded. The precise question at hand concerns the main stream *cities* only. It is the problem of balancing rural areas on the tributaries with urban areas on the main stream.

This is a problem of distributing people as well as distributing water. What should these mutual distributions be? This depends on the ultimate objective. If the purpose is to maintain the commercial *status quo,* estimated in values of present vested property interests, then we arrive at one kind of answer. This would be the answer of the commercialist. If the purpose is to attain regional habitability, estimated in values of ultimate optimum human living, then we arrive at another kind of answer. This would be the answer of the human ecologist.

Various projects are under way (including those of the United States Government) for charting and controlling the flow and distribution of waters within the sphere or region of the Ohio River watershed. These projects automatically affect the flow and distribution, within this sphere and region, of the folks themselves or population.

These projects combine in varying degree the objectives of the commercialist with those of the human ecologist. The appraisal of these projects from the latter's standpoint would serve a very useful function. In this the final test, of course, would be the effect on optimum human living of the respective projects.

This test is readily broken down into a series of subtests. These would include the effects on healthful population densities, on the proper proportion of urban to rural population, on employment opportunities, on educational and recreational facilities, on the proper balance of urban, rural and primitive settings.

Herein we have a very practical and immediate job for the human ecologist (or regional planner) in case he should desire to undertake it. It would serve as a useful check on the engineer, the forester, and the other land-use specialists. It would indeed complement their efforts. Such an

appraisal would make a working problem in "applied human ecology" as we have defined it.

The problem described is perhaps the most pointed and timely illustration that can be cited of the subject of this paper. Hence its use to show by example what the present writer has in mind by his definition of regional planning and its relation to the broader field of human and total ecology.

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HUMAN ECOLOGY AND HUMAN SOCIETY

By

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I regard my part in this symposium to be especially difficult, because the nature of the subject impels me to speak both as an ecologist and a sociologist; a peculiarly knotty problem since it is impossible to find a modicum of agreement among either the ecologists or the sociologists on just what is included in their disciplines (Alihan, 1938). I might add hastily, this is not a unique predicament for as Adams has remarked, only a generation ago plant and animal ecologists were in the same corner in their relations to the botanists and zoologists, who believed the taxonomic was the only order in nature (Adams, 1938). Keeping the limitations associated with the present theoretical state of ecology and sociology in view, this paper has been limited to three points: 1. A brief statement on the growth and differentiation in human ecology; 2. What we have taken from plant and animal studies; and 3. How we have dealt with the fact that in human society culture plays the role of adaptive structure and instinct in animal society, in so far as it limits and organizes the activities of individuals in the interest of society.

I. The Origin of Human Ecology

The first studies in the United States were made by Galpin in southern Wisconsin during 1910-1911 (Galpin, 1912, 1914, 1915). He demonstrated how the economic, political, and cultural interests of a communal area are integrated around the village where farmers trade. About this time social workers were making elaborate surveys of social conditions in our large cities with one eye on trying to explain the causes for slums, poor housing, and so on, and the other on alleviation of such conditions through the establishment of welfare agencies (Harrison, 1931). These ideas were combined in the series of studies of metropolitan areas in Chicago which were started about 1916 under the direction of Park, but they did not appear until the middle of the following decade when they were first integrated for the 1924 annual meeting of the American Sociological Society (Park and Burgess, 1925).

During the ensuing years hundreds of studies have been published on American communities and more are in process. Meanwhile, the ecological viewpoint has caught on in Europe, Asia, and Africa where several regional investigations have been completed. The emphasis in this country has been upon some aspect of the local community, but abroad practically all studies have taken the region as a frame of reference. In spite of its growing pop-

ularity, human ecology is too new a science, if I may be permitted this privilege, to be a regularly recognized academic discipline. To my knowledge, not a single university has a department, and only a few give courses under the title, although almost all introductory sociology courses include its main points in their subject matter.

Studies generally recognized as ecological fall into five broad classes: demography, migration, territorial organization, dominance and succession. Stated briefly, each emphasizes the following points:

1. *Demography* (McKenzie, 1933b). Viewed from a broad perspective this may include all the multiform data associated with population statistics which are evidence of the competitive strivings of men to maintain and reproduce themselves (Edge, 1928; Green, 1932; Clark and Gist, 1938) such as the distribution of population territorially, economically, and functionally (Gee, 1929; Baker, 1928).

2. *Migration.* The competitive process sifts men into areas and occupations where they can live better and more easily than in some other sector (Carpenter, 1935; Kennedy, 1930). Therefore, migration is one of the ways men individually and severally seek to adjust themselves to their habitat (Holmes, 1937; Beynon, 1938). Men migrate for many reasons, but most move on in search of a better place to live (Ferenczi, 1929; Thompson, 1931; Heberle, 1929). Migration brings into existence differentiated areas, and classes in the community (Bowman, 1926) as well as a stable ecological and social order, in short, equilibrium as we use the term (Krout, 1931; Park, 1928; Taylor, 1936).

3. *Territorial Organization.* The competitive process inherent in the market inevitably creates the division of labor between individuals and areas. Territorial distribution is a product, for as individuals and families, as well as industries seek the spot where they may most effectively compete, specialization and segregation necessarily occur (Rolph, 1932; Bossard, 1934). Culture, which enables man to coordinate his thoughts and actions, encourages this process, so he organizes the territory he occupies and works (Park, 1925; Haig, 1925). In our socio-ecological system, organization of territory binds every individual and area into a functional network on a local, communal, national, and in many ways an international scale (Harlan, 1935; McKenzie, 1933a). It is this fact which gives to a city, a village, or a rural countryside its typical spatial and functional patterning.

4. *Dominance.* Culture facilitates territorial organization, for it enables a few individuals and a relatively small area to dominate the activities in the competitive area organized by the market (Park, 1926; McKenzie, 1927). The function of dominance, exercised either by men or a position in the community, is to impose order among the competing units, and to insure a measure of stability in the dominated area (McKenzie, 1933b). The foregoing remarks indicate there are two orders of dominance: that of man; and of

position. The dominant position is the place where more men and services can concentrate than elsewhere, which gives the area competive advantages over other areas (Pratt, 1911). This draws to it still more men and services who seek these advantages; New York City is such a center. Dominant men are those who have the intelligence, skill, and power to direct economic and cultural activities.

5. *Succession.* Demographic, economic, and technological changes in a communal area or a region operate in response to new competitive conditions (Lind, 1938) and bring in their wake migrations, new activities (McKenzie, 1929), a new population (McKenzie, 1929), perchance complete decay (Lazarsfeld-Jahoda, 1933). Succession is the study of the form, order and effect of such changes on the functional, spatial and sustenance relations as well as the structure in any territorial unit (Burgess, 1926; Hollingshead, 1937) that has a function and plays a role in the organization of the area whether it is a section of a community (Leighly, 1928; McKenzie, 1933b), the larger organization of the region (Park, 1936), or speaking sociologically of the nation.

II. Our Debt to Plant and Animal Ecology

Human ecology is heavily indebted to plant and animal ecology for most of the three essentials to every science: *viewpoint, conceptual framework,* and *terminology.* This situation may be explained by the fact that it developed later than the other branches of the field, and like many a new discipline, borrowed extensively. Park, Burgess, McKenzie, and their associates combined the techniques of the social survey and Galpin's work on the rural community with the ecological viewpoint as it grew up under the influence of Warming, Adams, Clements, Cowles and others, then applied the terminology these men had used in describing the ecological relationships among other life forms to the phenomena discernible in the organization and structure of metropolitan Chicago. The work done by these men has been accepted as the point of departure for human ecology so that at the present time their ideas dominate the field. Those pioneers freely requisitioned concepts and terms previously established by plant and animal ecologists for use in the human field. For instance, aggregation, the biotic community, competition, dispersion, distribution, dominance, equilibrium, gradients, invasion, migration, succession, sustenance linkage, territorial organization, and the web of life are representative borrowed concepts now generally used by ecologically minded sociologists. Concentration, centralization, the occupational pyramid, community nucleus, market, position, hinterland, by way of contrast, are concepts independently developed. We must acknowledge this debt and recognize how astute our predecessors were rather than apologize for this wholesale borrowing. That this terminology and conceptualization are applicable to human phenomena should not be viewed as noteworthy for, after

all, man is only one species in the web of life, and so far as I know there is no reason to maintain, because he possesses a culture, we must or should place him in a compartment, then build around this fact a body of unique terms and concepts. It is only by viewing life whole (Phillips, 1932) that we are able to place man organically and functionally in the planetary scheme.

III. ECOLOGY, CULTURE AND HUMAN SOCIETY

The lines separating the general field into the present tripartition are polarized by the different ways plants, animals, and man, the unique mammal, have adapted themselves to the "struggle for existence." Relations between the symbiants in the plant community are purely economic, we might say almost mechanical, for there is apparently no fellow feeling, collective action, familial, or instinctive relationships, so prevalent in the animal world. Plants grow, reproduce, and die in a strictly vegetable manner (Clements, et al., 1929). Animals, on the other hand, are both structurally and instinctively adapted to their habitat (MacGintie, 1939; Wheeler, 1937). Among the higher animals is found the mating process (Carpenter, 1934; Tinbergen and Kruyt, 1937), a genetic family (Alverdes, 1927), collective action (Tinbergen, 1939), and mobility. The two facts that higher animals do mate, form families (Adams, 1908, 1918), and, second, act more or less collectively in response to genetically transmitted instincts (Emerson, 1939) are of great importance to the animal ecologist, but they mean little to the sociologist for the collective behavior observable among insects, birds, and mammals is not socially organized in the sense in which this term is used by the sociologist. From the literature I have gathered the conclusion that collective animal behavior is organized within the confines of the species' instinctive behavior pattern (Tinbergen, 1939; Emerson, 1939) without learning entering into the complex in more than an exceedingly limited and rudimentary degree. By way of contrast, in the case of man, structural differentiation is practically nonexistent, and instincts, if there are any, have been either replaced or sublimated through the development of socio-cultural organization (Linton, 1935; Cooley, 1902; Adrian, 1937). *Culture and socially organized behavior forms transmitted through learning, subsequent to birth, are the elementary factors that differentiate human from animal society.* Man only has evolved culture and developed techniques for transmitting it from generation to generation through associative learning, rather than the germ plasm, which enables him to adjust himself to almost any habitat (Malinowski, 1937; Sapir, 1934; Bowman, 1934). Culture then is a surrogate among men for the structural and instinctive mechanisms which have been set forth as an explanation for the type of collective behavior observed among ants (Wheeler, 1923), bees (Elton, 1927), wasps (Allee, 1931), birds (Adams, 1908; Alverdes, 1927), cattle (Austin, 1906), and other species. Since man is organically fitted into the web of life the same as other species, his sustenance

activities bring him into vital contact with his fellows, other organisms, and the physical environment in a manner comparable in many ways to the ecological relations recorded for other forms of life. Unlike other organisms though his competitive relations are confined within the locus of culture, therefore, the ecological aspects of society are always related to the strictly social ones.

When the sociologist *recognized* there were two intricately interdependent aspects of man's collective life, the ecological and the social, he was faced with the problem of discovering, analyzing, and interpreting the role each plays in human society. This problem has not been solved by any stretch of the imagination for it is almost impossible to find any agreement as to what constitutes the strictly ecological and cultural aspects of society; nevertheless, now that the problem is recognized and a beginning made we may expect a solution. At any rate the following paragraphs outline briefly how the problem has been attacked.

Speaking abstractly there are two orders in society derived from the basic types of interaction found among men when studied from the viewpoints of ecology and sociology (Park, 1938). They are what we may call, for lack of a more precise terminology, the ecological and sociological orders (Hollingshead, 1939a). The former is primarily an extension of the order found everywhere in nature, whereas the latter is exclusively, or at least almost, a distinctly human phenomenon (Reuter and Hart, 1933). The ecological order is primarily rooted in competition, whereas social organization has evolved out of communication (Park, 1938, 1939). The temporal and spatial identity of the community, the functional relations of the habitants to each other, as well as important phases in the life history of the individual, may be largely explicable through the observation and interpretation of the competitive relations that obtain between men and their environment as they function within the limits imposed on them by their culture. This competitive order takes the form of the division of labor—a purely symbiotic relationship—in which the interests of the participants are generally wholly selfish, impersonal, and non-social (Dawson and Gettys, 1935). The sociological order is based, by way of contrast, on communication between persons participating in groups (Sapir, 1934; Cooley, 1902; Quinn, 1934); a process which leads to more or less complete sublimation of the individual's interests and activities into the associated, collective interests and activities of the society (Park, 1938). Communication, therefore, entails behavior between persons who are conscious of themselves, their interests and aims, and who work out by consent and common action a program and a policy to achieve their collective ends (Chapin, 1935). Competitive association brings about the peculiarly selfish individuation of the person (Park and Burgess, 1925), while on the contrary, communicative association creates solidarity, *esprit de corps,* a consensus in which the individual, at least theoretically, strives to realize the

common goal. Custom, tradition, and institutions are all products of the consensus evolved out of the various forms of communication that exist between the several discrete members of a communal population aggregate socially organized for collective action (Hughes, 1936). Communication enables men functionally associated in the symbiotic process to get together intellectually and emotionally, and to transmit to each other ideas, experiences and techniques which become a part of the common culture to be used, cherished, and taught to strangers and children (Park, 1938; Hollingshead, 1939b). The sentiments, practices and beliefs derived from communication then bind men into a society; competition distributes them spatially and functionally into areas and combinations where they more or less effectively meet their organic needs.

From the dual viewpoints of (1) society's control over the individual, and, (2) the integration of collective action (Brown, 1926), society, as a result of the interactions between the competitive and communicative processes, may be viewed as a continuum organized on three interdependent levels which begins in the impersonal, ecological order, and ends with the highly rationalized, formal, and sentimental institutional order (Park, 1925, 1936, 1939). These integrative levels may be graphically represented by a pyramid divided into zones. The least restrained, and in many ways, non-social area of human action is discernible in competitive interaction, comparable in many ways to what is observed in the world of plant and animal symbiosis. Immediately connected with this is the informal order of moral organization rooted in inter-personal obligations. Finally, there is the sphere of institutional organization where formal social restraints define and limit societal behavior. Differentiation between each interactional area is determined by the type of social relations and restraints impinging on individuals as they function in the great society. Chart I should aid us to visualize the interrelations between the ecological and the two levels of the social order, for each compliments and supplements the other in many ways, as the vertical arrows indicate.

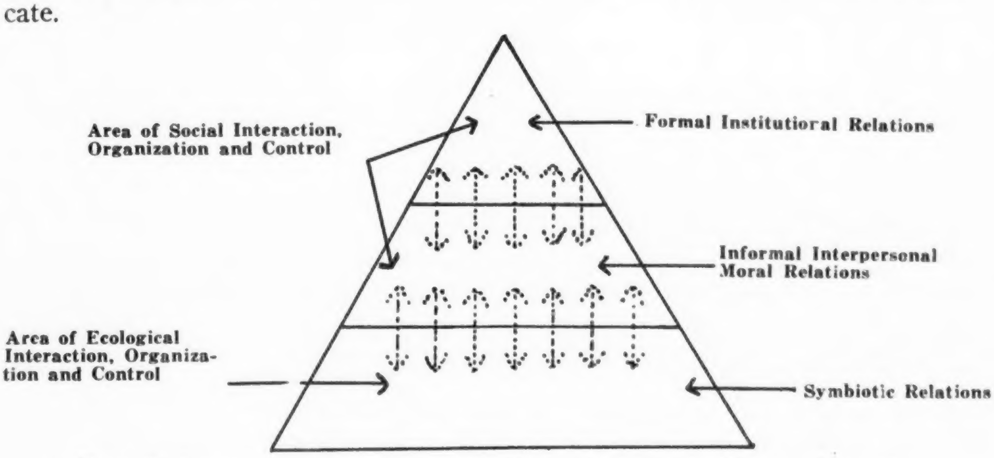

Chart I. LEVELS OF INTEGRATION AND ORGANIZATION IN HUMAN AFFAIRS.

The ecological order is rooted in individual adjustments to the conditions of life through the division of labor which exists between individuals, the sexes, age groups, and functional classes. The division of labor is a culturally determined sustenance system which enables man to satisfy his physiological needs partly within the confines of the symbiotic system prevailing among the lower organisms, and partly within the framework of a purely cultural organization (Reuter, 1939). Manufacture, trade, finance, and transportation are all cultural devices which make it possible for man to integrate his activities over wide areas, in a manner not seen or possible among plants and animals. By and large, the competitive position of the individual in a communal sustenance system determines pretty definitely his social status, income, place of residence, associates, and social activities (Hughes, 1938). In short, an individual's occupational connection places him both ecologically and socially in the community, a condition which more or less rigidly limits his activities within the confines of the socio-ecological system (Zorbaugh, 1926, 1929; Cavan, 1927; Cressey, 1932). For example, a W. P. A. laborer occupies a precise position in the community's sustenance linkage, his and his family's social status flows largely from this, he is limited rather rigidly as to place of residence, kind of residence, use of leisure time, and institutional participation. On the other hand, a banker occupies a different niche in the sustenance system, consequently a social status for him and his family arises from his ecological position; he has a residence, plane of living, and social relations proper to his station in life. The competitive process operating through the human mechanism of economic organization acts as an impersonal agency which distributes individuals *territorially* into the different parts of the community such as the farm, the factory, the store, the office, the slum, the working man's district, the palatial suburb (Zorbaugh, 1929), and *socially* into the several classes such as the elite, the upper middle class, the white collared menials, the poverty stricken (Hughes, 1938).

Although competition distributes individuals as we just indicated, communication manifested in economic practices integrates their activities, and makes it possible for man to specialize and concentrate his efforts on a minute function, yet by the process of exchange to satisfy his physical and social needs in a cooperative manner without organic structural differentiation taking place (Wirth, 1929; Lynd, 1929, 1937). Competition, also, segregates economic and social services into areas where they can best survive. The operation of this broad principle gives to the ecological aspects of the community their characteristic physical patterning: the central business district, the adjacent deteriorated slum areas, railroad yards, apartment areas, sections of beautiful homes, and the outlying open country. The distribution of individuals spatially and territorially is to a large extent a product of the competitive struggle for life and creates an area's social structure in comparison with other areas in the community. The impersonal organization of

individuals through the division of labor and the market may be viewed as a surrogate for organic adaptation among other forms of life. Lastly, by way of summary, competition is the organizing ecological process; division of labor is the human counterpart of structural and instinctive adaptation among other organisms (Reuter, 1939).

The moral order grows out of the fact that persons in intimate association accumulate informal usages, customs, traditions, and values which become more or less obligatory behavior forms to be followed in their relations with one another (Hollingshead, 1939b). This is a purely social process for the individual is no longer just an interactional unit, but a person with status, a role, and responsibilities to his fellows. In short, he is a member of a group, therefore, he must conform to the group's behavior codes. Self is submerged to group, and the person becomes an integral part of society. Interpersonal group obligations must be observed or the person loses status, is snubbed, becomes frustrated, unhappy, maladjusted, and in severe cases is ostracized as being immoral or insane. Group obligations limit personal behavior within the group to such an extent that lusty animal drives or personal desires have to be repressed in the interest of personal happiness and group solidarity (Hollingshead, 1938b). On this level, communication has reached such a high degree of rapport that persons in intimate contact day after day are able to anticipate common thoughts and actions of the participants in the relationship. This fusion of self into the association is discernible in any highly organized group such as an army, a profession, a gang of thieves (Sutherland, 1937), the Communist Party (Doob, 1935), or a family. That this progressive submergence of self to society is not a healthy process from the viewpoint of the organism is beginning to be recognized by the psychiatrist.

On *the institutional level* relations between persons, groups, and classes have become formal, rationalized, and accepted as sanctioned usages common to the society. Family, church, school, business, state, and other institutions have evolved in response to the need for a functionally differentiated society to regulate social relations so society can act as an organized unit. This necessitated the formulation of societary rules for the express purposes of defining the relations of persons to one another, to things, and ideas, on a more formal, direct basis than is found in the moral order. Social institutions from the viewpoint of social organization and control are positive regulatory devices set up by society to limit behavior practices (Hertzler, 1929; Hughes, 1939). These behavior standards are implemented by social machinery such as laws, courts, and administrative officers.

Social relations within the areas of moral and institutional organization are in juxtaposition to ecological relations. The social process by placing its primary control emphasis on the continued well-being of group and society places individual existence in a subordinate relation to its welfare. The ecological process as found in the plant, and to a less extent in the animal

realm, is focused on the preservation of the individual, and only incidentally the community. The social process emphasizes the need to preserve the society, which is essentially a social form, rather than the individual. There is then a natural antithesis between the individual as an organism, and as a member of society. As an organism his own needs come first, as a person his obligations to the society are paramount. Groups and institutions explicitly and implicitly limit the organism's desires through moral responsibilities, law, and all other forms of authority the society can exert to sublimate selfish individual aims into social ideals. But it is only as a member of society that the organism can realize his physiological needs, a fact which inextricably places man in a position of symbiosis and sociability.

IV. Concluding Remarks

By way of conclusion, I shall enumerate a few points entailed in the past and future growth of human ecology.

1. A recognition of the fact that ecologically man is a part of the web of life, therefore, connected with other organisms and the physical environment.
2. Sociologically he is a species apart, because of his cultural heritage which enables him to socially organize his behavior in a unique manner.
3. The ecological aspects of society are rooted in the competitive struggle for life, the sociological ones in communication between the competitors. Communication results in the organization of social relations on a moral and an institutional level where the activities of the person are increasingly controlled in the interests of society.
4. Human activities restrained within the confines of social considerations result in the social aspects dominating the ecological ones. This creates an antithesis between the ecological and social orders which frequently gives rise to man's unwitting destruction of the balance of nature in the pursuit of social ends and values thereby creating pathological conditions in the individual and society.
5. Some unsolved problems before the ecologist and the sociologist are:
   a. To determine precisely the ecological activities of the individual in relation to others, to the habitat, and conversely, the nature and scope of the interdependency between the ecological and social orders;
   b. To discover the influences changes in ecological organization have on social organization, and vice versa.
6. Finally, we have to devise methodological techniques which will enable us to objectively discover and measure these and other variables.

If what I have said smacks too much of the armchair, I beg you to remember as a sociologist I have but four decades of history behind me, as a

human ecologist barely two; while you as biologists have thirty decades of history, as ecologists, four or five.

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ECOLOGY: AN INSTRUMENT FOR THE INTEGRATION OF SCIENCE AND PHILOSOPHY

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Our purpose as scientists and philosophers is to "get at" reality. It is not necessary, I hope, to seek justification for this common purpose: the search for reality and the search for truth, these are inherent qualities of human nature which come to the fore whenever and wherever conditions are favorable.

We possess perceptual capacities which allow us to see reality in particulars, and we also possess conceptual powers which reveal realities in their larger and more general settings. The various disciplines which we have developed for this purpose, perceptually and conceptually (scientifically and philosophically) have not, unhappily, enjoyed equal or parallel progress. The sciences have moved forward steadily for at least three centuries. Philosophy, on the contrary, is still episodic, personal, and cyclical. The search for reality has been far more successful than the search for truth. It is not surprising, therefore, to discover that the more mystical forms of philosophical thought have re-asserted themselves even in our time, that is, in a period of heightened scientific success.

It appears that philosophy has suffered most as a consequence of this unequal development. In fact, the disparity is so great that ours has been called the scientific age. If anyone were to name it the philosophical age, he would, no doubt, be laughed to scorn. But, I wish to remind you that the rout of philosophy has not been complete. There exists an American strain of thought, a philosophical tradition which has always maintained a double focus, that is, an awareness of both fact and morality, a regard for what is, and what should be. Peirce, James, and Dewey have laid the foundations of this philosophy and it is to be noted that the younger philosophers who have followed the lead of this triumvirate have taken great pains to orient themselves in the sciences before embarking upon the task of philosophical generalization. In fact, I now feel quite safe in asserting that most of our younger pragmatic philosophers know a great deal more about science than most of our leading scientists know about philosophy. Scientists of all varieties do, of course, philosophize since every generalization is in a sense philosophical and it is impossible to engage in genuine scientific thought without generalizing. Indeed, I wish that some of our leading scientists would subject their social, economic, and political generalizations to more rigorous philosophical tests

before submitting them as guides to public action. As a sample of the way in which trained scientists disregard the more simple rules of evidence when they generalize I shall save myself some embarrassment, perhaps, if I choose a European rather than an American as illustration. Professor Lenard of the University of Berlin, a former Nobel Prize winner, has recently published his definitive work on physics. This formidable two-volume essay is entitled *Deutsche Physik,* and in explanation of this unusual admixture of nationalism and science, Professor Lenard writes in his preface: "I might rather have said Aryan physics, or physics of the Nordic species of man. Physics of the seekers after truth, the very founders of science. But it will be replied to me that science is and remains international. This I say is false. Science like every other human product is racial and is conditioned by blood." I have chosen an almost ludicrous illustration of what may happen when a trained physicist enters the field of ethnology but I hope that the extremity of my example will not destroy its usefulness: similar fallacies in reasoning occur too frequently for comfort when capable scientists become publicists in the sphere of human purposes, moral values, and social movements. My fear is based upon the assumption that the current prestige of scientists is so great as to render their philosophical statements immune from criticism.

I wish there were no artificial barriers between the various sciences nor between science and philosophy so that we might all move from objectivity to subjectivity, from the particular to the general, and finally from theory to practice in order that both science and philosophy might become collaborating instruments on behalf of human progress.

Three terrifying wars are now in process in Europe and in Asia. These are, perhaps, the first truly technological wars of history; their potentialities for destruction are so great that it is not unreasonable to suppose that the culmination might mean a devastation so vast and so comprehensive as to bring civilization itself to an end. The warring nations have appropriated both science and philosophy as instruments for attaining their ends. The haunting question which now disturbs sensitive citizens, both scientists and laymen, may be stated thus: Is it likely that science has become the handmaiden of modern warfare because scientists have in the past neglected those moral issues on behalf of which men will, in desperation, fight and kill? And, is it likely that modern propaganda, the chief ally of war, has become so cleverly philosophical because philosophers in the past have overlooked the moral implications of scientific facts, especially scientific facts transmuted into technology? In short, may it not be true that these wars are in themselves demonstrations of the presumption that the chief difficulty of our era is a consequence of the persistent separation between science and philosophy, between what is and what should be?

My answer to this basic question has been reached by an arduous process of reasoning which has spanned a long period of time but most of my misgivings have at last been dispelled and I can now state with vigor that it is

my conviction that human progress depends upon collaboration between science and philosophy. I can foresee no beneficent culmination of the human experiment unless those who deal with facts are also concerned about the use of facts, and unless those who deal with values understand that values in order to become effective must be reconciled with facts. Otherwise, that is, if facts and values remain dissociated, the very instruments designed by science for our good will be used to destroy us, and the values which might give stability to our culture will become objects of contempt and sources of cynicism.

I have already placed myself outside the restricted realm of scientific statement since I am asking you as scientists to give attention to that which should be rather than that which is. I make no apology for this "transgression" because it is not my intention to leave the problem at this point. On the contrary, I now propose to use my value-statement as an hypothesis, and in this respect, at least, I behave as a scientist. How may scientists and philosophers work together? How may the disciplines of fact and value become complementary? What experiments might be conducted for the purposes of including both facts and values?

Since both science and philosophy are based upon assumptions there is already considerable over-lapping which needs to be more candidly recognized. Scientists utilize philosophical assumptions and philosophers use scientific assumptions and although the ratio of indebtedness is unequal the responsibilities are mutual. The first of these responsibilities is to strive for better understanding between the two groups. We must first of all understand each other if the public is to understand either or both of us. I repeat what was said at the outset of this essay, namely, we are both striving to "get at" reality and hence if we are to work together, we must understand each others' language.

What we are attempting to do in this symposium needs to be multiplied many times. Our presiding officer, Dr. Adams, has set for us a shining example. In his paper dealing with the "Relation of General Ecology to Human Ecology" (*Ecology*, Vol. 16: 316-335) he reminds us that every objective situation may be examined from at least three vantage-points. Taking his clue from Whitehead (Adventures of Ideas) he suggests that reality may be viewed, first of all, through the microscope of the unit sciences, that is, by means of an observational approach; but, in most cases, this approach has already been conditioned by the telescopic vision of the philosopher, or the conceptualist. These seemingly diverse viewpoints should not, however, be considered as antitheses, as so often happens; on the contrary, these are interacting elements in a combined process of inquiry. In short, science and philosophy are complementary, not competitive tools.

It is not wholly accidental, I believe, that this suggestion has come from an ecologist. Ecology is the study of the relation of organisms to their complete environment. It is then in itself a relational discipline. Why should

anyone wish to understand the relation between organisms and environments? Obviously, such inquiry is pointed toward a value question, namely: does the existing relation work out to the advantage of the organism, or does it not? The moment this query is placed upon the human level and we begin to inquire into the relation between man and his complete environment we begin to see that the instruments of investigation required must be furnished by both science and philosophy. The scientists may say that any relation between man and his environment which permits survival is also satisfactory but the philosopher will demur: the philosopher will remind the scientist that nations are even now waging wars for the purpose of space (Lebensraum) and for access to raw materials; he will, if he is a collaborator in the inquiry, insist that every human ecological situation is shot through and through with moral issues. He will go even further; he will insist that this is likely to be more true of the future than it has been of the past. Modern science, in its technological aspect, is an effective destroyer of natural ecological balance. Indeed, it may even be said that one of the chief lessons to be learned from the application of technology to human affairs is this: it tends to weaken if not to destroy all natural, automatic controls. Each step forward in the use of science and technology as instruments of human adjustment calls for an expansion of consciousness, or in other words, for increased social planning.

The papers delivered at this symposium combine to substantiate my thesis: taken separately or together they represent an equation which places the various unit sciences at one pole, social planning at the opposite pole, and ecology in the middle. A sound ecological viewpoint of any given human situation involves all available factual knowledge which the various sciences are capable of revealing but facts so far interfused and integrated as to present a situational whole which includes both organisms (human beings) and the related environment. When the sciences are able to present wholes of this character to the public it will be possible to posit alternatives of action designed to bring about a progressive series of dynamic balances. From this point onward, social planning will not need to rely upon *a priori* or ideological patterns of social organization; its foundations will rest solidly upon scientific findings; social planning may then rid itself of all absolutistic doctrines and proceed in genuine experimental fashion.

In the above project I have assumed that the ecological viewpoint serves to integrate the various unit sciences. Its true function begins in that middle ground where the physical and biological sciences leave off and the social sciences begin. When the ecologist is able to describe a situation in terms of its combined human and environmental aspects he has, in fact, accomplished an integration of the sciences. The chief by-products of an enterprise of this sort would be: (a) the physical and biological scientists would achieve social orientation, and it is conceivable that they might also come to view the primary end or purpose of science to be human welfare, and (b) the social

scientists would learn how to bring their social theories into functional relations with the "hard" facts which are brought to the surface when organisms are studied conjointly with their interacting environments.

In my eagerness to show how ecology might become the instrument for integrating the sciences I seem to have lost the philosophers. They must now be brought back into the equation since my generalized proposition is that human welfare cannot be assured until science and philosophy function confluently.

Social planning as I conceive it is a method through which human beings are to perform a function which in a pre-scientific age was left largely to Nature itself. Social planning represents a conscious attempt on man's part to establish a dynamic balance between himself and his environment, or stated more bluntly, social planning is a means for using science as an instrument for human welfare. As a means it will be used, for example, to prevent the waste of natural resources, to direct our resources, both material and human, towards social ends. All scientists engaged in social planning would, therefore, be utilizing science in the public interest.

In the above paragraph I have employed at least two words which are definitely philosophical, namely *human welfare* and *public interest.* The moment one begins to speak of ends, goals, or values, it is at once apparent that we have entered upon the domain of philosophy. From this step onward, unhappily, there will be certain separations. Those who insist that they have no concern for human welfare, nor for human purposes or ends, will now depart our company. Their absence will bring sadness to me because I feel so strongly that they must, even those who are most rigorously scientific in their outlook, help us to determine ends and goals. If they do not, others who are not scientifically-minded and who have no respect for truth will formulate the goals. And, I have a strong suspicion that the goals imposed upon us by absolutists and dictators will constitute an unhappy day for science. Those scientists who refuse to accept social responsibility have already been sorely exploited by private interests. They will be exploited to an even greater degree by totalitarian states in which freedom itself is disqualified. Where there is no freedom, both science and philosophy will be degraded until each becomes a mere tool in the hands of skilled propagandists and wilfull demagogues.

Hence, I lay before the ecologist who is interested in the relation between science and society still another obligation. I have already asked him to keep in mind both the physical and biological sciences on the one hand and the social sciences on the other. I now beg him also to include philosophy as an integral part of his design. The ecologist stands in a most advantageous position. He has already acquired the habit of dealing with wholes as well as fractions. To this extent he is a philosopher. If he now invites philosophers to become his collaborators, especially at those points where he views his ecological findings as preparatory to social planning, he may expect two

varieties of guidance. The philosophers will watch for those elusive but fateful moments when *means* are brought into juxtaposition with *ends,* and he will be insistent that the means shall be consistent with the ends. Over and over these philosophers will say: "Be careful! Good ends cannot be attained by the use of bad means." You, the ecologist, will then ask the philosophers to describe *good ends,* since you both will have agreed that science is a "good" means because it has already demonstrated that it is the most satisfactory problem-solving device thus far invented by man. You will also have agreed that a great deal more of science will be needed if man is to discover a better relation with his environment.

If you have been fortunate in the choice of your cooperating philosophers, you will now find to your surprise that you can still speak a common language. Your philosophers, if they have not been too far divorced from human affairs and from science, will reply that the ends and the values of life are also matters to be determined by experimentation. They will begin the quest for values by inquiring what it is that human beings basically need. Next, they will ask you to give as accurate a statement as possible regarding the capacity of the existing environment to fulfill these needs. They may then invite you to join in the enterprise of arranging these needs in the order of their relative importance, first for survival, and later for a sufficient life. Before long you will both be involved in discussions concerning the alterations in the environment or the conditionings in human beings which are required in order to meet certain needs and to realize certain values. In short, you will be cooperating in the task of formulating conscious ecological experiments for the purpose of improving the human situation. I cannot understand why scientists and philosophers should shrink from participation in experience of this variety. On the contrary, it appears to me that integrated experiences of this sort, experiences which would tend to humanize the sciences and to practicalize philosophy, might readily be seen as the golden opportunity for bringing a new rationalism into our distracted world.

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FACTORS CONTROLLING THE EARLY DEVELOPMENT AND SURVIVAL OF EASTERN WHITE PINE (*Pinus strobus* L.) IN CENTRAL NEW ENGLAND

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FACTORS CONTROLLING THE EARLY DEVELOPMENT AND SURVIVAL OF EASTERN WHITE PINE (*Pinus strobus* L.) IN CENTRAL NEW ENGLAND[1]

INTRODUCTION

The purpose of this investigation was to measure the changes that occur in the site factors of white pine stands under different degrees of cutting and to ascertain the influence of these changes on the early development and survival of white pine seedlings.

Observations have shown that, although adequate reproduction usually occurs in abandoned fields and meadows near seed trees, it is almost entirely lacking in the interior of pure white pine stands. Heavy seed crops occur at intervals of 3 to 7 years, but young pine reproduction rarely develops with sufficient vigor to replace the mature stand after logging. When pure pine stands are clear cut, hardwood growth which has become established as advance reproduction usually develops on the cutover area. Since pine yields better than hardwoods on the lighter soils and frequently brings a greater financial return, it is often desirable to obtain pine reproduction in the development of new stands.

Previous investigations relating to the problem of the natural regeneration of forest stands have shown the importance of the changes in site conditions which are brought about by logging. These studies show that even a relatively light cutting may alter the various site factors and decidedly influence seedling reproduction. The plan of investigation adopted in this study involved the establishment of a series of quadrats of white pine seedlings under three different conditions of cover in the white pine region of central New England. Certain climatic and edaphic factors were measured periodically throughout two growing seasons. Seedling development and survival were correlated with site factors at each station in order to determine the effect of different degrees of exposure on the reproduction of this species.

The investigation covered in this report was initiated in the autumn of 1932 while the writer was engaged in graduate study in the Yale School of Forestry. During the school year 1932-1933, the work was carried on under the direction of Ralph C. Hawley, Morris K. Jesup Professor of Silviculture, Yale University, and J. L. Deen, Instructor in Silviculture, then in Yale University. The investigation was continued in 1933-1934 under the guidance of Professor Hawley and H. J. Lutz, Assistant Professor of Forestry, Yale University. The writer acknowledges his indebtedness to these men

[1] Contribution No. 153, Department of Horticulture, Kansas Agricultural Experiment Station.

for valuable assistance and advice in planning the field work and in preparation of the manuscript. Acknowledgments are also due J. S. Boyce, Professor of Forest Pathology, Yale University, for the identification of damping-off diseases; Roger B. Friend, Assistant Professor of Forest Entomology, Yale University, for the identification of certain rodents; and to J. Paul Miller, Junior Biologist of the Bureau of Biological Survey, United States Department of Agriculture, for the identification of a number of small animals. The writer is also grateful to Oran B. Stanley, Gregoire Leclerc, and J. B. Ely for assistance in connection with the field work.

The field experiments were established in the Yale Demonstration and Research Forest near Keene, New Hampshire, and the field data obtained during the summers of 1933 and 1934. The experiments in this investigation were arranged after the method described by Haig (1936) in a study of the factors controlling initial establishment of western white pine and associated species in Idaho. Similar procedures were adopted in order that the silvical factors influencing the early development of eastern white pine might be compared with those found to be most important in the early development of a related western species. The writer is also indebted to Dr. I. T. Haig for advice and suggestions in the establishment of the field experiments.

The original manuscript covering this investigation was submitted as a dissertation in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Yale University.

ENVIRONMENTAL CONDITIONS AND PROCEDURE

Arrangement of Experiment

The arrangement of the field experiment involved the establishment of seedling quadrats under three conditions of exposure in natural white pine stands. One half of the quadrats were on natural pine litter and the other half at each station on mineral soil from which the litter had been removed. The three stations represented full shade conditions under a complete canopy, partial shade in a thinned stand and full sun on a cutover area. Instruments were employed at the three stations during the growing season to measure site factors. Seedling losses were determined through two growing seasons. Significant site factors were measured and their relation to seedling mortality and development determined.

Description of Stations

The three areas selected for this study were located on the alluvial plain of the Ashuelot River in the Yale Demonstration and Research Forest near Keene, New Hampshire. They were less than one half mile apart and were essentially alike except in the amount of overhead canopy. The full-canopy station was in a dense irregular-aged white pine stand in which the trees

FIG. 1. Reproduction near the margin of an evenaged stand of white pine. Note increase in size and vigor of pine toward the background. Although seedlings appear following a seed year, no reproduction has become established in the interior of this stand. City Park, Keene, New Hampshire.

FIG. 2. A dense group of white pine reproduction developing in an opening. Showing uniform gradation in height with increasing distance from the overwood. Yale Forest, Keene, New Hampshire.

varied in size from 1.7 inches to 14.8 inches in diameter breast high. The average diameter in this stand was 4.6 inches and the average height of the dominant trees 44 feet. The part-canopy station was located in a pure pine stand, 41-60 years old, in which approximately one half of the dominant trees had been cut in the winter of 1931-1932. In 1933 the basal area at the full-shade station was 315.8 square feet per acre. At the part-shade station standing timber with a basal area of 126.5 square feet was present in 1933 and 81.2 square feet in 1934. This difference in density of stand for the two seasons was caused by locating the station in 1934 a short distance from that of the previous year in an effort to obtain undisturbed soil conditions. The open station was established on an area that was clear cut in the winter of 1931-1932. A stand of pine in which there was a light admixture of hemlock and hardwoods was removed at that time. After the cutover stations were logged, various species of hardwoods as well as shrubs and herbaceous plants appeared on these areas. All woody vegetation in the vicinity of the seed quadrats was cut back in order to eliminate its effect upon seedling growth.

Soil Conditions

The primary rock of the region in which the investigation was conducted has been described as chiefly protogene gneiss of hornblende schist, mica schist, and quartzite (Toumey, 1932). The soils of the valley in which the stations were located developed from glacial drift. They are composed chiefly of fine to coarse sand with a small proportion of gravel. Boulder deposits are present in the valley, but they were found sparingly only at the part-canopy station of the areas under study. Although these soils are considered too sandy to support a vigorous growth of hardwoods, they seem well adapted for white pine which has been successfully established throughout the region on similar soils. As the soil particles are coarse and the surface sloping, drainage takes place rapidly. This condition in addition to high evaporation during summer months may result in pronounced droughts during periods of light rainfall.

The physical character of the surface soils as determined by mechanical analysis shows a high proportion of sand fractions. The percentage relationship of the various size classes is presented in Table 1.

Table 1. Comparative Characteristics of Horizon A for Three Stations

Station	Mechanical analysis (fractions in percent)			Hydrogen-ion concentration	Wilting coefficient
	Sand	Silt	Clay	pH values	(percent)
1 (complete canopy)	87.2	8.9	3.9	5.02	6.81
2 (partial canopy)	70.6	20.2	9.2	5.02	10.53
3 (open)	77.8	15.6	6.6	5.20	8.75

The proportion of sand fractions in the soils at the different stations as shown in Table 1 is 70.6 percent for the part timbered area, 77.8 percent in the open and 87.2 percent under the complete canopy. This high proportion of sand particles clearly indicates a low water holding capacity and also that such soils will not retain moisture well during periods of drought.

The hydrogen-ion concentration of a given soil often influences physical and biotic reactions and may directly affect plant growth. The quinhydrone electrode method was employed to determine the pH values of air-dried soil samples. These values are presented in Table 1 and are in good agreement for the three stations and may be considered to be well within the range for optimum white pine development as shown by Sundling, McIntyre, and Patrick (1932).

The wilting coefficient marks the theoretical lower limit of soil moisture available for plant use and consequently is a useful measure in studies of water relations in plants. In this study, the usual procedure was followed in obtaining this soil moisture relationship. It involves the determination of the moisture equivalent by the method devised by Briggs and Shantz (1912). Samples of surface soil from the three stations were run in triplicate to obtain the moisture equivalent and the wilting coefficient was calculated by using the ratio proposed by the same authors. The values obtained in this way show that the wilting coefficient determinations are closely correlated with soil texture as shown in Table 1. The wilting coefficient values were 6.81 in full shade, 10.53 in part shade and 8.75 at the full sun station.

In order to make a further comparison of the influence of the soils from the different stations on seedling development, blocks of soil approximately 5 inches thick, with the litter intact, were carefully lifted, placed in flats, removed to the greenhouse and sown to white pine. After germination, the seedlings were grown for 6 months under similar conditions of light, temperature, and moisture. At the end of this period, there was no apparent difference among the plants grown on soils from the different stations.

STATION EQUIPMENT

At the beginning of the growing season, a battery of weather instruments was installed at each station (Figs. 3, 4, and 5). The instruments in use included a hygrothermograph, maximum and minimum thermometers, soil thermometers, Livingston type of black and white atmometer spheres, anemometers, rain gauge, and psychrometer. Equipment was also available for soil moisture determinations.[2] Daily records of habitat conditions were obtained throughout two growing seasons at the three stations. These readings included maximum and minimum soil temperatures which were taken at the depth of 2 inches. In addition, maximum and minimum surface tem-

[2] As only two hygrothermographs were available in 1933, daily air temperature and relative humidity readings were obtained with current thermometers and a sling psychrometer at the part canopy station during this season.

FIG. 3. Station 1. Anemometer in foreground. Instrument shelter with thermograph and hydrograph partly shown on left. Atmometer and surface thermometer at left center. Two reproduction plots in the center and one at the right in the foreground. Remaining plots are in background. Note dense canopy and scanty ground vegetation.

FIG. 4. Canopy at Station 2. Plots located under the canopy on the left.

FIG. 5. Station 3. Showing a part of the instruments used during the 1933 season, Livingston atmometers and anemometer. Hygrothermograph in instrument shelter. Seedling plot in foreground.

FIG. 6. A number of the instruments at Station 3. Livingston black and white atmometers, maximum and minimum surface soil thermometers. Maximum and minimum soil thermometers and current soil thermometers.

peratures were obtained on both litter and mineral surface types. Insolation intensity and evaporation were measured with Livingston porous cup atmometers. Paired black and white spheres were installed at each station with the instruments exposed as shown in Figure 6.

PROCEDURE

In the autumn of 1932, an equal quantity of white pine seed was sown on a number of quadrats 3 feet square at each station. Three quadrats were sown on the undisturbed pine litter and three on mineral soil from which the litter had been removed. Sufficient seed was used to obtain approximately 100 seedlings per square foot. The quadrats were covered with screen frames over winter to exclude rodents. In the spring of 1933, two more quadrats were established on litter surface and two on mineral surface at each station.[3] In order to eliminate drought as a possible killing agent, one litter and one mineral surface quadrat at each station were watered during dry periods throughout the first season.

After germination began in the spring, the screen frames were removed and were used thereafter only when rodents were found invading the quadrats. Germination counts were made daily and each new plant marked with a wooden pin. Losses were also recorded daily and the cause of mortality determined by the appearance of the dead seedlings, supplemented by current weather records and soil moisture determinations. When the causal

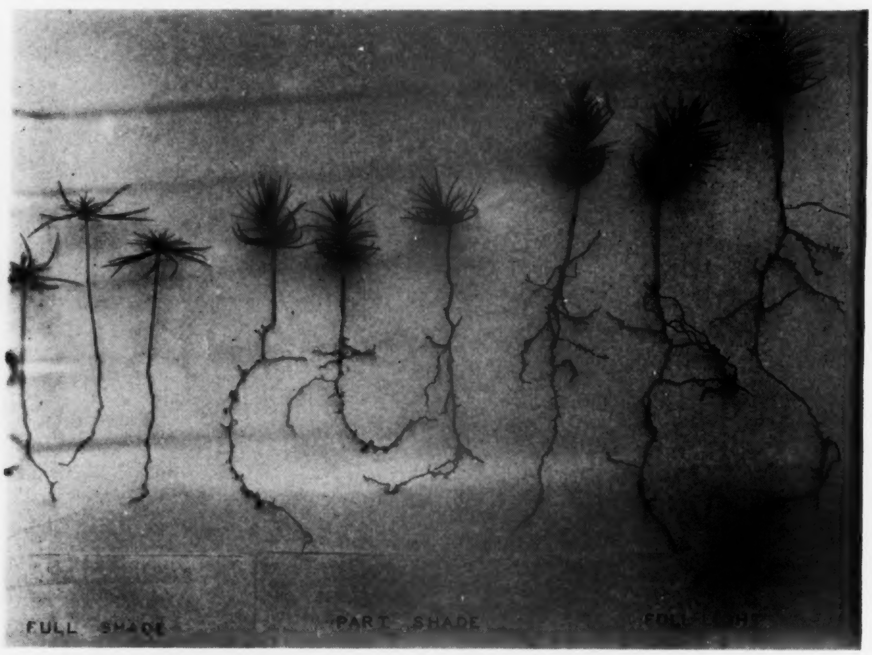

FIG. 7. One-year-old seedlings from the 3 stations under study. Left, Station 1. Center, Station 2. Right, Station 3.

[3] Poor drainage at the part canopy station made it necessary to change this station to a new location in the spring of 1933. Consequently the ten quadrats at this station were spring sown.

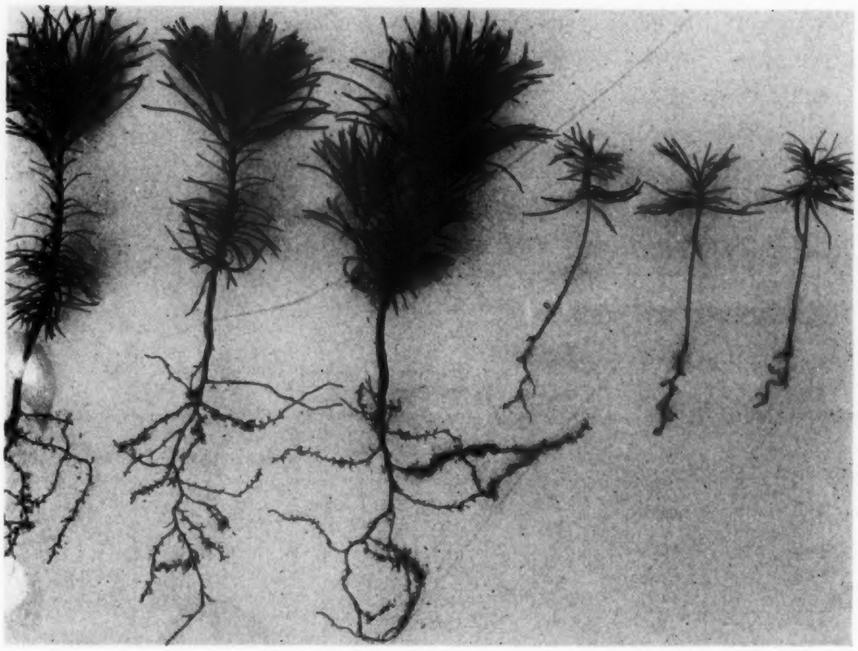

FIG. 8. Two-year-old seedlings grown on mineral soil. Left, Station 3. Right, Station 1.

agency could not be determined, the losses were listed as unknown and later allocated to the major killing agencies in proportion to the importance of each such agency in causing known losses. Since the unknown losses were only a small percentage of the total this method did not greatly affect the final percentage values allotted to each of the major agencies of mortality.

In 1934, the experimental procedure was essentially the same as during the previous season. The principal difference in quadrat arrangement consisted in sowing all quadrats at the three stations in the autumn. Furthermore, the quadrats at the part shade station were located in a more open portion of the stand in order to avoid the disturbed surface conditions surrounding the 1933 quadrats. This change in location resulted in slightly greater exposure of the soil surface in 1934.

SEASONAL CONDITIONS IN 1933

General Character of Growing Season

In order to evaluate growing conditions for the 1933 season, monthly precipitation and air temperature were compared with the normals for the region. These records showed that total rainfall, for the season, was 0.54 inches above normal. Nevertheless, the early part of the growing season including May, June, and July was subject to severe drought. These 3 months received less than 65 percent of the normal amount of rainfall. April

and August, however, were unusually wet receiving 3.45 and 3.20 inches, respectively, more than normal. Monthly precipitation and departures from the normal are presented in Table 2.

In this region, precipitation is usually rather well distributed throughout the year. A deviation in annual rainfall of more than 10 percent from the normal is infrequent. However, high evaporation and the low water-holding capacity of the sandy soils may cause severe drought in periods of low rainfall during the summer months and such conditions are likely to be especially critical for first-season coniferous seedlings.

TABLE 2. MONTHLY PRECIPITATION IN INCHES FOR THE 1933 GROWING SEASON COMPARED WITH THE 48-YEAR NORMALS*

Month	Normal for period	1933 Season	Departure	Departure
	Inches	*Inches*	*Inches*	*Percent*
April	3.19	6.65**	+3.46	(+108.4)
May	3.03	1.86**	—1.17	(— 38.6)
June	2.90	1.41**	—1.49	(— 51.4)
July	3.45	2.13***	—1.32	(— 38.3)
August	3.58	6.78***	+3.20	(+ 89.4)
Means	3.23	3.77	+0.54	(+ 16.7)

*Normals were taken from weather data for Nashua, New Hampshire, as records at the Keene station were available for only 8 years. Nashua is located approximately 50 miles southeast of Keene.
**Figures taken from weather records for Keene.
***Figures taken from open station records.

The conditions of surface soil moisture and surface temperatures directly influence germination and early spring survival of young seedlings. These factors are closely associated with amount of cloudiness and the frequency of rainfall. Data showing the number of cloudy days and days with precipitation are presented in Table 3.

TABLE 3. CONDITION OF SKY AND NUMBER OF DAYS WITH PRECIPITATION GREATER THAN 0.01 INCHES IN 1933*

Month	Number of Days			
	Clear	Partly cloudy	Cloudy	With precipitation
April	9	5	16	15
May	16	9	6	9
June	8	10	2	10
July	16	9	6	10
August	14	6	11	15

*Figures taken from weather records for Keene.

The monthly temperatures for the season with departures from the normals are presented in Table 4. Beginning with a mean of 43.7 degrees F. in April air temperature increased through the spring reaching a maximum during July and then gradually declined through August. The mean temperature for April was only slightly above the minimum heat requirement for

physiological plant functions. Consequently very little plant growth was observed during this month. The low air temperature affected the soil temperature so that insufficient heat was available to support germination of white pine seed until about May 15.

In 1933, the mean monthly air temperatures differed only slightly from the normals at Keene. The departures from the monthly normals seem too small to be considered significant in influencing plant growth and the growing season may be regarded as essentially normal in respect to air temperature.

In 1933, the last frost in the spring occurred June 2 and the first in the autumn on September 12. The frost-free period for this season was 102 days.

TABLE 4. MONTHLY TEMPERATURES IN DEGREES FAHRENHEIT FOR THE 1933 GROWING SEASON COMPARED WITH THE 8-YEAR NORMALS*

Month	Normal for period	1933 Season	Departure	Departure
	Degrees F.	*Degrees F.*	*Degrees F.*	*Percent*
April	43.8	43.7	—0.1	(—0.23)
May	55.4	56.9	+1.5	(+2.63)
June	63.6	65.1	+1.5	(+2.30)
July	68.9	68.6	—0.3	(—0.40)
August	66.2	65.8	—0.4	(—0.61)
Means	59.6	60.0	+0.4	(+0.67)

*Figures taken from weather records for Keene.

LIGHT CONDITIONS

Paired black and white Livingston atmometer spheres were employed at each station to determine daily radiation intensities. The atmometer reservoirs were lowered into the soil with the porous spheres approximately three inches above the surface where they would be exposed to insolation and wind action similar to that affecting small seedlings. The position of the instruments is shown in Figure 6. Haig (1936) found that these instruments give insolation intensity values which agree closely with determinations made with the Shirley thermopile and the Clement's photometer. Moreover, the Livingston spheres are well adapted for field use because of the simplicity of operation. An added advantage is that they record current changes throughout the day.

Light intensities reaching the forest floor at the timbered stations vary widely throughout the day due to the changing angle of direct insolation. Consequently the amount of light received at a given point on the soil surface changes during the day and also as the season progresses. Under these conditions of fluctuating light, duration of exposure, as well as the intensity at any given period, may become significant to plant growth.

Light intensity values were determined by subtracting the amount of water given off by the white atmometers from that lost by the black instruments. The values obtained in this way indicate the differences in radiation at the

three stations. When the sky was overcast, the black and white instruments agreed closely in the amount of water lost, but on bright days losses from the two types of instruments varied widely and were most divergent at the open station. Comparative water losses from paired instruments and their differences are presented in Table 5.

TABLE 5. MEAN DAILY EVAPORATION IN MILLILITERS BY MONTHS FROM POROUS CUP ATMOMETERS FOR 3 STATIONS IN 1933

Month	STATION 1 (complete canopy)			STATION 2 (partial canopy)			STATION 3 (open)		
	Black bulb	White bulb	Difference	Black bulb	White bulb	Difference	Black bulb	White bulb	Difference
June	12.95	12.13	0.82	17.33	14.77	2.56	33.65	23.82	9.83
July	10.12	9.54	0.58	14.68	12.47	2.21	29.48	20.52	8.96
August	6.38	5.96	0.42	9.30	8.12	1.18	20.96	13.80	7.16
September	2.83	2.62	0.21	4.04	2.79	1.25	15.03	8.43	6.60
Seasonal mean	8.07	7.56	0.51	11.34	9.54	1.80	24.78	16.64	8.14

These data show that light values were highest in June and gradually decreased throughout the remaining months of the growing season. The rate of decline, however, was much more rapid at the timbered stations than in the open. Early morning and late afternoon light becomes very weak in dense stands probably resulting in a diminished period of effective radiation for plants under canopies. This reduction in light duration under timber stands suggests that reproduction is not only subject to weak light, but also to a somewhat shorter daily period of effective light than open grown seedlings.

Seasonal light intensity values determined in percentages of full sunlight in the open were found to be approximately 6 percent at the full shade station and 22 percent at the part shade station. According to investigations by Shirley (1929, 1932), Gast (1930), Mitchell (1936), and Gast (1937) light intensity of 6 percent of full sun approaches the lower limit for survival and 22 percent is about the minimum for vigorous growth.

SURFACE TEMPERATURES

Both maximum and minimum temperatures on litter and mineral soil surfaces were determined with the goose-neck type of thermometers at each station. These instruments were placed approximately level with the surface and the bulbs covered with one-fourth inch of the surface material. One pair of instruments was installed on mineral surface and one on litter surface at each station. In 1933, instrument records were begun June 20.[4]

The most significant of the surface temperature records are presented in Table 6. It has been noted in the discussion of literature that surface tem-

[4] Germination, however, had begun prior to this time but arrangements could not be made to install the instruments at an earlier date.

peratures in excess of 120 degrees F. are likely to be critical for young coniferous seedlings. This critical value was exceeded only once during the season at the complete-canopy station. According to daily observations, there were no deaths from heat recorded on this occasion at this station. Although it is possible that temperatures above 120 degrees F. occurred on the more exposed portions of the part-canopy station, there were no other values as high as this recorded during the season. In 1933, the highest surface temperature occurring on the part timbered area was 114 degrees F. on litter surface June 29. As anticipated, surface temperature conditions were much more severe in the open and this proved to be the principal killing factor at this station.

The records show that in 1933 killing temperatures occurred 45 days on litter in the open, compared with 40 days on mineral surface. Furthermore, temperatures reached or exceeded 135 degrees F. for 23 days on the litter compared with 17 days on mineral soil. Because of the porous character of litter, evaporation occurs rapidly with a consequent increase of temperature above that of mineral soil. Consequently, killing temperatures may occur on exposed litter the first clear day following rain, but the better retention of moisture in the mineral soil precludes fatal temperatures on this surface type for a longer period. After the mineral soil becomes thoroughly dry, this difference in the two surface materials is reduced and the daily maxima tend to approach the same values.

TABLE 6. MAXIMUM SURFACE TEMPERATURE RELATIONS ON MINERAL AND LITTER SURFACES FOR 3 STATIONS IN 1933

Month	Station	Number of days on which these temperatures occurred				Daily maximum temperature in degrees Fahrenheit			
		120 deg. F. or above		135 deg. F. or above		Average		Highest	
		Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface
June	1 (complete canopy)	—	—	—	—	89	80	106	97
	2 (partial canopy)	—	—	—	—	93	96	103	114
	3 (open)	9	10	3	8	121	135	141	163
July	1 (complete canopy)	1	—	—	—	90	86	122	117
	2 (partial canopy)	—	—	—	—	91	91	110	111
	3 (open)	21	24	11	11	124	128	151	154
August	1 (complete canopy)	—	—	—	—	75	76	104	100
	2 (partial canopy)	—	—	—	—	85	85	106	104
	3 (open)	9	10	3	4	106	108	151	148
September	1 (complete canopy)	—	—	—	—	68	68	78	74
	2 (partial canopy)	—	—	—	—	85	82	102	96
	3 (open)	—	1	—	—	95	97	114	121

The highest maximum surface temperature for the season was 163 degrees F. on litter surface June 22. The highest reading for the mineral surface was 151 degrees F. occurring July 19 and August 2.

SOIL TEMPERATURES

Various writers, as previously indicated, have called attention to the importance of soil temperature in its reaction upon the germination of seed and the early growth of forest-tree seedlings. In addition to the direct effect in supplying heat for growth, soil temperature also influences the availability of water, the rate of chemical reactions in the soil and the activity of soil organisms. Inasmuch as soil receives heat both from the air and directly from solar radiation, soils in dense stands usually are colder than those in the open. Since the soil absorbs heat better than air, the temperature of surface soil layers in the open often exceed air temperature. In forests, however, where direct insolation is partly excluded by the canopy, heat from air currents is absorbed by the soil and therefore air and surface soil temperatures tend to be closely correlated during the growing season.

Germination of forest-tree seed does not begin in the spring until adequate heat becomes available in the soil. Pearson (1931) found that the amount of heat required to initiate germination in a number of coniferous species in the Southwest varied widely within the group studied. Adams (1934) suggests that late germination, resulting from inadequate soil temperature, may be a factor in the establishment of seedlings in forests.

Monthly soil temperatures, as presented in Table 7, were determined by computing the daily mean from the maxima and minima readings and then averaging these values for each month.

In 1933, the mean soil temperature for the season was 0.3 degrees F. lower on litter and 1.2 degrees F. higher on mineral surface in part shade than at the full shade station. In the open, however, the values were several degrees higher than at the part shade station. Observations also show that the mineral soil temperatures are slightly higher than those obtained on the

TABLE 7. MEAN MONTHLY SOIL TEMPERATURES IN DEGREES FAHRENHEIT AT 2-INCH DEPTH FOR 2 SURFACE TYPES AT 3 STATIONS IN 1933

Month	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)	
	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface
June	64.0	66.0	61.7	64.3	70.0	73.0
July	61.7	65.7	62.5	65.2	68.6	73.5
August	62.2	62.0	62.2	64.4	68.6	72.7
September	60.0	58.5	60.5	63.1	64.8	66.5
Seasonal mean	62.0	63.0	61.7	64.2	68.0	71.4

litter. Lower temperatures on litter-covered soils are probably caused in part by the insulating effect of the pine litter.

Pearson (1931) considers maximum temperature values to be more useful in determining the amount of effective heat available for growth since the mean temperatures obtained by averaging the daily maxima and minima give equal weight to the relatively ineffective night temperatures and the more effective day temperatures. Soil temperatures taken at 2 inches approach the same values under the canopy and in the open at night, but day temperatures are considerably higher in the open. He concludes that averaging the daily maxima and minima tends to minimize the effective day temperatures and does not adequately evaluate the greater amount of heat available in exposed situations.

The maximum monthly soil temperatures are presented in Table 8. These data show a greater difference in temperatures between stations than that expressed by the mean monthly values in Table 7. The monthly maxima in the open are approximately 12.9 and 19.0 degrees F. higher on litter and mineral surface, respectively, than soil temperatures in full shade. As soil temperatures under canopies in this region are low until late in the spring, this factor may be of considerable importance in delaying early seedling growth in shaded situations.

TABLE 8. MAXIMUM MONTHLY SOIL TEMPERATURES (DEGREES FAHRENHEIT) AT 2-INCH DEPTH FOR 2 SURFACE TYPES AT 3 STATIONS IN 1933

Month	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)	
	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface
June	64.8	—	66.1	70.1	81.4	88.2
July	67.1	—	67.1	73.0	81.8	88.0
August	68.2	68.8	67.4	73.8	80.4	86.9
September	65.9	65.0	65.3	72.9	73.9	80.7
Seasonal mean	66.5	66.9	66.5	72.4	79.4	85.9

SOIL MOISTURE

Although in this region precipitation is usually distributed uniformly throughout the growing season, drought periods of varying severity may occur during the summer months. The frequency of critical droughts is increased by rapid seepage of free water and rather high evaporation rate in clear weather. In 1933, May, June, and July were deficient in rainfall varying from 38 to 51 percent below normal. The heaviest shower in June provided less than one half inch of moisture. Furthermore, not until July 22 when 0.61 inch fell did the rainfall exceed one half inch. Examination of the surface soil showed that showers less than this amount were largely intercepted

by the canopy and litter at the timbered stations. Soil moisture records proved that soil moisture was deficient at these two stations until after July 22. The first inch of soil in the open under litter closely approached the wilting coefficient on this date. On litter quadrats in full shade, soil moisture remained near the critical condition until July 29.

Weekly moisture determinations for the first 3 inches of soil, as shown in Table 9, indicate the changes that occurred in this factor during the 1933 growing season.

TABLE 9. SOIL MOISTURE IN PERCENTAGE OF OVEN-DRY WEIGHT OF SAMPLE FOR 3 STATIONS ON 2 SURFACE TYPES IN 1933

Date	Depth of sample in inches	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)		PRECIPITATION	
		Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface	Date	Inches
June 25	0-1	18	10	—	—	—	—	June 22	0.42
	1-2	—	—	—	—	—	—	26	0.36
	2-3	—	—	—	—	—	—	30	0.04
July 2	0-1	—	—	—	—	—	—	July 5	0.15
	1-2	12	10	19	14	19	21	9	0.20
	2-3	—	—	—	—	—	—	10	0.23
8	0-1	—	—	—	—	—	—	20	0.61
	1-2	8	12	11	16	18	14	21	0.31
	2-3	—	—	—	—	—	—	22	0.09
15	0-1	7	5	13	10	18	12	25	0.47
	1-2	6	7	10	11	15	16	30	0.07
	2-3	10	7	9	11	13	13		
22	0-1	8	22	14	28	9	25		
	1-2	6	18	14	18	15	16		
	2-3	7	17	15	17	17	18		
29	0-1	13	13	15	20	18	20		
	1-2	12	13	14	17	16	17		
	2-3	11	12	15	16	15	16		
Aug. 5	0-1	18	22	14	34	12	22	Aug. 4	1.41
	1-2	19	22	13	26	10	21	8	0.18
	2-3	21	20	13	22	19	10	13	0.96
12	0-1	13	14	17	21	15	14	14	0.67
	1-2	14	13	16	15	14	13	17	0.08
	2-3	11	12	16	14	14	14	18	0.60
19	0-1	24	24	—	33	18	23	19	0.63
	1-2	24	22	20	25	—	24	22	0.28
	2-3	23	20	21	23	21	25	24	1.85
26	0-1	26	29	22	30	26	26	29	0.12
	1-2	27	26	20	23	26	24		
	2-3	24	25	19	21	25	22		
Sept. 2	0-1	20	20	19	21	22	21	Sept. 3	0.28
	1-2	22	20	25	21	20	20	4	0.87
	2-3	21	19	21	21	20	20	6	0.80
9	0-1	26	27	38	—	28	—	7	0.53
	1-2	23	27	29	30	30	—	9	0.20
	2-3	24	26	24	27	27	30		

SEASONAL CONDITIONS IN 1934

GENERAL CHARACTER OF GROWING SEASON

In 1934, rainfall was 0.58 inch above normal for the five growing months. Deficiencies occurred only in May and August with departures of 26 and 7 percent, respectively, below the monthly averages for the region. In general, precipitation was well distributed throughout the season resulting in favorable soil moisture conditions throughout most of the growing period. In contrast to the 1933 season, June and July rainfall exceeded the normal amount and May showed a smaller deficiency than in the preceding season. As the period immediately subsequent to germination, before extensive root development has taken place, is the most critical, this season was definitely superior to 1933 in regard to moisture. Monthly precipitation values and departures from the 48-year normals are presented in Table 10.

TABLE 10. MONTHLY PRECIPITATION IN INCHES FOR THE 1934 GROWING SEASON COMPARED WITH THE 48-YEAR NORMALS*

Month	Normal for period	1934 Season	Departure	Departure
	Inches	*Inches*	*Inches*	*Percent*
April	3.19	4.05**	+0.86	(+27.0)
May	3.03	2.25**	—0.78	(—25.7)
June	2.90	5.41***	+2.51	(+86.5)
July	3.45	4.03***	+0.58	(+16.8)
August	3.58	3.32***	—0.26	(— 7.3)
Means	3.23	3.81	+0.58	(+18.0)

*Normals are for Nashua, New Hampshire.
**Figures taken from weather records for Keene.
***Figures taken from records for the open station.

Although there were fewer cloudy and rainy days in 1934 than during the previous season, the precipitation was greater and more evenly distributed. Soil moisture determinations show that increased precipitation more than compensated for the drying effect of the greater number of clear days during this season.

TABLE 11. CONDITION OF SKY AND NUMBER OF DAYS WITH PRECIPITATION GREATER THAN 0.01 INCHES IN 1934*

Month	Number of Days			
	Clear	Partly cloudy	Cloudy	With precipitation
April	14	8	8	11
May	19	6	6	8
June	19	7	4	13
July	20	7	4	7
August	23	3	5	9

*Figures taken from weather records for Keene.

In 1934, mean monthly air temperature showed only small variations from the monthly normal. The greatest variation occurred in August which was 3.3 degrees F. below normal. The seasonal mean temperature of 59.6 degrees F. was equal to the normal for the five growing months at Keene. It seems probable that the departures of monthly temperatures from the normals are too small to be significant in affecting seedling growth. In 1934, the frost-free period for Keene was 116 days. Monthly temperatures and departures from the normal are presented in Table 12.

TABLE 12. MONTHLY TEMPERATURES (DEGREES FAHRENHEIT) FOR THE 1934 GROWING SEASON COMPARED WITH THE 8-YEAR NORMALS*

Month	Normal for period	1934 Season	Departure	Departure
	Degrees	*Degrees*	*Degrees*	*Percent*
April	43.8	44.7	+0.9	(+2.05)
May	55.4	56.8	+1.4	(+2.53)
June	63.6	64.8	+1.2	(+1.87)
July	68.9	69.0	+0.1	(+0.15)
August	66.2	62.9	—3.3	(—4.98)
Means	59.6	59.6	0	0

*Figures taken from weather records for Keene.

LIGHT CONDITIONS

Light intensity, as determined from readings of the Livingston atmometer spheres, was approximately the same at the full-shade and full-sun stations in 1934 as in 1933. The part-shade station, however, received more light in 1934, as the quadrats were unavoidably located in a more open portion of the stand the second season. The reason for this change in location has been previously explained. Comparative daily insolation data as obtained by the black and white bulb atmometers at the three different stations are presented in Table 13. The highest average light values occurred during July at all three stations. May and June, however, were only slightly lower than July, and August and September showed an appreciable reduction below

TABLE 13. MEAN DAILY EVAPORATION IN MILLILITERS BY MONTHS FROM POROUS CUP ATMOMETERS FOR 3 STATIONS IN 1934

Month	STATION 1 (complete canopy)			STATION 2 (partial canopy)			STATION 3 (open)		
	Black bulb	White bulb	Difference	Black bulb	White bulb	Difference	Black bulb	White bulb	Difference
May	15.20	14.36	0.84	20.58	15.92	4.66	35.54	24.69	10.85
June	10.45	9.72	0.73	16.10	12.86	3.24	27.56	17.41	10.15
July	12.65	11.74	0.91	19.59	14.14	5.45	31.05	19.56	11.49
August	7.99	7.43	0.56	13.23	10.17	3.06	22.50	14.09	8.41
September	5.80	5.42	0.38	13.40	9.02	4.38	18.54	11.18	7.36
Seasonal mean	10.42	9.73	0.67	16.58	12.42	4.16	27.04	17.39	9.65

the values for July. The seasonal radiation intensities were approximately 7 percent at the full-shade station and 43 percent in part shade of that in the open.

In comparing the light intensities in 1934 with the values of the previous year, it may be noted that insolation intensity was approximately 1 percent greater in full shade and 21 percent greater in part shade than in 1933. As previously indicated, this increase in radiation at the part-shade station is due to locating the quadrats in a more open portion of the stand the second season.

SURFACE TEMPERATURES

In 1934, daily records of surface temperature were begun May 16 and continued to September 5. As early as May 16, a reading of 134 degrees F. was recorded for the litter surface in the open compared with a maximum value of 99 degrees F. the same day on the mineral surface. A number of comparative maximum temperature values on the two surface types at the 3 stations are presented in Table 14. These data show that during this season no reading as high as 120 degrees F. was obtained at the full-canopy station. At the part-canopy station, however, temperatures critical for seedling survival were exceeded 17 days on the litter surface, although no temperature as high as 120 degrees F. was obtained on the mineral surface. On four

TABLE 14. MAXIMUM SURFACE TEMPERATURE RELATIONS ON MINERAL AND LITTER SURFACES FOR 3 STATIONS IN 1934

Month	Station	Number of days on which these temperatures occurred				Daily maximum temperature in degrees Fahrenheit			
		120 deg. F. or above		135 deg. F. or above		Average		Highest	
		Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface
May	1 (complete canopy)	—	—	—	—	80	87	103	108
	2 (partial canopy)	—	1	—	—	86	96	110	127
	3 (open)	—	13	—	7	95	128	109	151
June	1 (complete canopy)	—	—	—	—	72	79	101	106
	2 (partial canopy)	—	10	—	3	86	101	117	136
	3 (open)	2	24	—	18	97	128	129	165
July	1 (complete canopy)	—	—	—	—	86	91	102	106
	2 (partial canopy)	—	6	—	1	98	105	111	139
	3 (open)	25	27	8	25	125	139	154	162
August	1 (complete canopy)	—	—	—	—	73	—	86	82
	2 (partial canopy)	—	—	—	—	81	89	97	114
	3 (open)	15	21	1	8	110	120	138	143
September	1 (complete canopy)	—	—	—	—	69	—	72	—
	2 (partial canopy)	—	—	—	—	79	88	84	94
	3 (open)	—	3	—	1	103	119	116	136

of the days with critical temperatures in partial shade, readings on the litter reached or exceeded 135 degrees F. At the open station, there were 88 days on the litter surface and 42 on mineral soil with temperatures above 120 degrees F. Furthermore, temperatures of 135 degrees F. or greater occurred 59 days on litter compared with only 4 days of similar temperatures on mineral soil. The highest surface temperature recorded for the season was a maximum of 165 degrees F. on litter June 30.

These extremely high temperatures emphasize the importance of insolation in the mortality of young seedlings, both on the part-timbered area and in the open. Natural pine litter proved to be a decidedly more unfavorable surface for reproduction than mineral soil. This difference between the two surface types was more pronounced in 1934 than in the preceding season. The greater severity of the litter surface may be attributed to more favorable rainfall during the second season. It was observed that the litter dried rapidly on clear days following rain and seedlings on this surface type were almost immediately exposed to critical temperatures. On the mineral surface, desiccation takes place more slowly thereby reducing the number of critical days. Consequently, the more uniform precipitation in 1934 reduced the number of days with critical temperatures on mineral soil to a greater extent than on litter surfaces.

Soil Temperatures

In 1934, soil temperature readings were begun May 15. Germination began May 16 in the open and at the part-shade station. The first seedlings appeared at the full-shade station May 23. At the open station, the mean maximum soil temperature for the first five days was 66 degrees F. and the mean minimum for this period was 45 degrees F. Similar temperatures for the same period at the other stations were 55 and 45 degrees F. in part shade and 52 and 40 degrees F. in full shade. The mean daily temperatures for this period were 55 degrees F. in the open, 50 degrees F. in part shade and 46 degrees F. in full shade or a difference between stations of about 5 degrees F. at the time germination began.

TABLE 15. MEAN MONTHLY TEMPERATURES IN DEGREES FAHRENHEIT AT 2-INCH DEPTH FOR 2 SURFACE TYPES AT 3 STATIONS IN 1934

Month	Station 1 (complete canopy)		Station 2 (partial canopy)		Station 3 (open)	
	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface
May	49.5	49.1	52.3	52.7	57.7	59.5
June	58.4	58.8	59.7	61.0	65.9	66.9
July	64.2	65.0	65.1	65.2	70.6	71.1
August	59.8	60.9	60.4	61.4	67.8	67.2
September	57.0	57.2	58.4	59.0	64.0	65.4
Seasonal mean	57.8	58.2	59.2	59.9	65.2	66.0

Soil temperatures increased through May and June, reaching their maximum values in July at all stations. After July, temperatures declined through August and September.

The canopy reduced the mean soil temperature approximately 8 degrees F. in full shade and 6 degrees F. in part shade below that in the open.

When the maximum temperatures were averaged, the full-shade station was found to be 13 degrees F. and the part shade 11 degrees F. lower temperatures than at the full-sun station.

TABLE 16. MAXIMUM MONTHLY SOIL TEMPERATURES IN DEGREES FAHRENHEIT AT 2-INCH DEPTH FOR 2 SURFACE TYPES AT 3 STATIONS IN 1934

Month	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)	
	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface
May	55.3	55.6	57.1	59.3	67.8	66.2
June	63.2	63.2	65.5	66.5	75.4	75.9
July	69.4	70.9	70.5	71.5	82.4	82.5
August	63.8	64.7	65.5	66.6	77.0	76.1
September	60.2	61.4	61.8	63.0	72.6	72.6
Seasonal mean	62.4	63.2	64.1	65.4	75.0	74.7

In 1934, soil temperatures were secured at the depths of 6 and 12 inches at the full-shade and open stations. The monthly means are presented in Table 17. These records show that temperatures were approximately 10 degrees F. higher at each depth in the open than under the full canopy.

TABLE 17. MEAN MONTHLY SOIL TEMPERATURES IN DEGREES FAHRENHEIT AT 6-INCH AND 12-INCH DEPTHS FOR 2 STATIONS IN 1934

Month	STATION 1 (complete canopy)		STATION 3 (open)	
	6 inches	12 inches	6 inches	12 inches
May	48.3	43.2	60.2	55.9
June	58.3	55.9	68.1	64.0
July	63.3	61.2	74.3	70.0
August	60.6	56.3	69.9	67.2
September	57.4	55.8	65.6	63.0
Mean	57.6	54.5	67.6	64.0

SOIL MOISTURE

In 1934, seasonal rainfall was above normal and in general well distributed throughout the growing season. Available soil moisture did not become deficient during the early part of the season which is usually the most critical period for young seedlings. The amount of soil moisture present in each of the upper 3 inches of soil is shown in Table 18. These data show

that the first drought period began July 14 and continued until a rain of 2.19 inches fell on July 27. On July 14, soil moisture was below the wilting coefficient in the first inch of soil of the mineral quadrats at the part-shade and full-shade stations and also at the open station on July 21. According

TABLE 18. SOIL MOISTURE IN PERCENTAGE OF OVEN-DRY WEIGHT OF SAMPLE FOR 3 STATIONS ON 2 SURFACE TYPES IN 1934

Date	Depth of sample in inches	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)		PRECIPITATION	
		Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface	Date	Inches
May 19	0-1	31	26	26	35	30	28	May 21	0.04
	1-2	27	24	27	31	28	27	22	0.05
	2-3	23	25	26	28	30	29	25	0.08
26	0-1	21	26	24	22	37	33	26	0.02
	1-2	24	24	22	20	26	27		
	2-3	24	14	24	22	24	27		
June 2	0-1	22	11	25	—	40	22	June 2	0.86
	1-2	18	16	22	13	28	26	3	0.46
	2-3	16	17	35	27	11	24	4	0.72
9	0-1	26	22	29	20	32	32	6	0.36
	1-2	23	23	26	27	26	27	9	0.05
	2-3	21	23	30	26	26	27	10	0.03
16	0-1	21	27	38	45	48	33	12	0.67
	1-2	20	28	31	38	32	26	13	T
	2-3	22	25	31	24	29	26	14	0.37
23	0-1	25	26	38	43	51	43	16	0.21
	1-2	25	26	34	29	32	34	19	1.40
	2-3	20	28	31	27	28	28	23	0.19
30	0-1	23	20	22	13	61	18	25	0.09
	1-2	20	19	26	17	35	24	27	T
	2-3	19	19	23	27	31	23		
July 7	0-1	20	16	32	14	41	11	July 2	0.10
	1-2	18	15	26	20	22	22	3	0.50
	2-3	18	16	24	21	21	23	5	T
14	0-1	8	5	13	5	10	13	13	0.04
	1-2	9	9	15	10	18	12	14	0.34
	2-3	9	10	15	12	21	17	20	0.02
21	0-1	9	9	17	8	16	8	21	0.01
	1-2	11	11	13	12	13	12	27	2.19
	2-3	10	11	13	13	12	12	28	0.71
28	0-1	10	19	21	20	20	36	31	0.12
	1-2	16	24	20	23	22	21		
	2-3	17	22	20	23	34	23		
Aug. 4	0-1	24	28	22	27	42	23	Aug. 2	0.03
	1-2	23	23	22	25	24	20	3	0.83
	2-3	22	25	26	23	24	19	12	0.10
11	0-1	18	19	19	—	21	24	13	0.06
	1-2	19	20	24	17	22	21	16	0.42
	2-3	18	20	22	17	20	19	22	0.88
18	0-1	23	23	32	12	13	38	24	0.48
	1-2	20	20	27	16	18	21		
	2-3	18	20	24	19	17	20		
26	0-1	14	21	28	40	38	14		
	1-2	17	20	23	28	27	19		
	2-3	16	19	22	28	26	19		

to the weekly determinations, moisture in the second two inches of soil was never reduced as low as the wilting coefficient. Nevertheless, in dry periods, drought loss in weak plants might occur on the driest portions of the quadrats. Differences in crown density and variations in depth of litter were largely responsible for lack of uniformity in surface soil moisture.

Evidently the dense stand of pine was an important factor in the greater reduction of soil moisture at the full-shade station during dry periods. After a heavy rain, which occurred on July 27, adequate moisture was available for seedlings throughout the remainder of the season.

SEEDLING GROWTH AND LOSSES IN 1933

The records of site conditions at the 3 stations were markedly different for the season in respect to light, air temperature, surface temperature, and soil moisture. Moreover, these differences in the intensity of site factors were reflected in the germination and development of seedlings at the different stations. Germination was most complete at the full-shade station. Here the heavy shade early in the season tended to maintain favorable surface moisture, resulting in prompt germination of fall-sown seed on the mineral surface as soon as suitable temperatures were reached. Although germination began almost as early on the litter as on the mineral surface, it was not as complete on the former, but continued during rainy periods throughout the season. Table 32 shows that there is a moderate difference between germination on litter and mineral surfaces at the full-shade station. The quadrats at the part-canopy station were spring-sown, resulting in later germination than the fall seeding at the other two stations. The difference in germination on the 2 surface types was not statistically significant. The greater exposure in part shade accompanied by higher evaporation resulted in a lower percentage of germination than under the full canopy. In the open, a marked contrast was manifest between the amount of germination on litter and mineral surfaces. Exposed litter tends to dry rapidly on clear days so that insufficient moisture was available to support germination. This condition resulted in the appearance of only 16 seedlings on litter compared with 1,959 on mineral soil at the open station. The comparative germination data for the 3 stations are presented in Table 19.

Two quadrats at each station, one with mineral and one with litter surface, were watered during the 1933 season in order to eliminate deficient soil moisture as a factor in survival. These quadrats were spring-sown, therefore are not strictly comparable with the fall seeding at the full-shade and open stations. Watering resulted in more uniform germination on all quadrats with the exception of litter surface in the open. Watering was not beneficial here as it was impossible to maintain sufficient moisture with one daily application to support germination. Germination figures for the watered quadrats are shown in Table 20.

TABLE 19. GERMINATION BY MONTHS FOR 2 SURFACE TYPES AT 3 STATIONS IN 1933

Month	STATION 1* (complete canopy)		STATION 2** (partial canopy)		STATION 3* (open)	
	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface
May***	—	—	—	—	—	—
June	1,079	3,320	—	—	16	1,953
July	212	67	1	377	—	1
August	66	6	94	189	—	—
September	3	2	21	4	—	5
Total	1,360	3,395	116	570	16	1,959

*3 fall-sown quadrats for each surface type.
**4 spring-sown quadrats for each surface type.
***The amount of germination in May was not determined as the quadrats were not under observation during that month. Germination for June includes May also.

TABLE 20. GERMINATION BY MONTHS FOR 2 SURFACE TYPES OF SPRING-SOWN, WATERED QUADRATS IN 1933*

Month	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)	
	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface
June	—	—	—	—	—	—
July	203	278	206	155	—	149
August	338	190	215	103	—	51
September	4	1	5	—	—	3
Total	545	469	426	258	—	203

*1 quadrat for each surface type.

The early development of seedlings immediately following germination was observed to differ widely in the shade and in the open. Full-shade plants had longer stems but the deep pigmentation characteristic of full-sun plants was lacking. This contrast became more marked as the season advanced. The shaded seedlings for the most part failed to develop secondary leaves or to increase appreciably in stem diameter. In contrast to this etiolated condition of full-shade seedlings, those in the open developed shorter, thicker stems and continued to put forth new foliage throughout the season. Gast (1937) found that when radiation was reduced to low intensities for Scotch pine and white pine seedlings, the plants remained in a succulent condition throughout the season. Moreover, periodic examination of the root system proved that root growth was retarded even more than shoot development. The same author also reported that if radiation intensities up to 22 percent were provided, most of the food is supplied to shoots. At higher intensities, an increasing proportion is made available for root growth.

At the part-shade station, plant growth was less vigorous than in the open, however, both top and root growth continued throughout the summer

and the plants developed normally in respect to a balanced shoot-root ratio. The comparative size of the plants on the three areas is shown in Figure 7.

The comparative mortality by the different killing agencies is presented in Table 21.

TABLE 21. COMPARATIVE SEASONAL LOSSES BY AGENCIES IN PERCENTAGE OF TOTAL LOSS FOR 2 SURFACE TYPES AT 3 STATIONS IN 1933*

Agency	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)	
	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface
Heat	—	—	—	61	100	100
Drought	79	93	—	—	—	—
Insects	5	1	100	15	—	—
Fungi	16	6	—	24	—	—
Losses in percentage of germination	42	27	15	16	94	39

*Rodent losses were not included in computing percentage of losses by different agencies.

High surface temperature was the principal killing agent in the open. Heat injury was usually noted by the presence of lesions which developed on the stems immediately above the soil surface. The appearance of these lesions was commonly followed within a short time by death of the plant. In some cases, the xylem continued to function for several weeks after girdling had taken place. When this occurred, the plant remained alive through a part of the season. In a small proportion of injured plants, the lesions occurred only on one side of the stem. In some instances, these injured plants completely recovered.

All heat injury occurred within a period of a few weeks following germination. Open-grown seedlings suffered heavily early in the spring, but the plants which escaped injury at that time developed cortical tissue which rendered them immune to excessive temperatures later in the season.

Surface temperatures were more severe in the open on litter than on mineral surface. This difference could not be completely evaluated in its effect on mortality since very few plants germinated on litter surface at the open station. All of the seedlings on litter, however, except one were killed by heat early in the spring. Approximately 39 percent of the seedlings on mineral surface were killed by excessive surface temperatures. This proved to be the only physical agency active in seedling mortality at the open station during the first season. According to statistical test as shown in Table 33, the difference in heat mortality on litter and mineral quadrats was not significant. This result is undoubtedly influenced by the small number of seedlings germinating on litter at this station. High surface temperatures were less severe at the partial-canopy station than in full sun. Shade provided by

overhead canopy at this station reduced the severity of insolation as an agent in mortality. Some 61 percent of the losses on the mineral surface quadrats were due to excessive heat, but no deaths from heat were recorded on litter at this station. This can probably be attributed to heavier shade over litter quadrats rather than to beneficial effects of the litter surface. In 1933, the full-shade station was entirely free from losses which could be directly attributed to heat.

During the 1933 season, drought was an important killing agent only in full shade. At this station, approximately 79 percent of the losses on litter quadrats and 93 percent of those on the mineral soil were directly attributed to this factor. The statistical analysis of drought losses in Table 33 does not show a significant difference between seedling losses on litter and mineral quadrats. The major portion of these losses occurred in June and July. During this period, soil moisture was reduced below the wilting coefficient as shown in Table 18. Moreover, the weak root development of full-shade seedlings prevented them from keeping pace in elongation with desiccation of the surface soil. In 1933, there were no losses at partial-canopy and open stations which could be directly attributed to drought. The part-shade and open-grown seedlings which survived the high surface temperatures developed vigorously both in top and root. Seedlings at these stations were characterized by thick, short stems, vigorous leaf growth and extensive root development. On account of this vigorous growth, root penetration occurred more rapidly than downward desiccation of the surface soil and consequently drought losses did not occur even during the driest part of the season.

The biotic agencies, active in destroying seed and seedlings, included rodents, insects, and fungi. Red squirrels (*Sciurus hudsonicus* Erxleben), northern white-footed mice (*Peromyscus leucopus noveboracensis* Fischer), domestic mice (*Mus M. musculus* L.), and chipmunks (*Tamias striatus striatus* L.) invaded the quadrats at various times and destroyed seedlings in searching for ungerminated seed. Prompt measures were taken to control animal damage as soon as it was observed. Whenever rodent damage was detected, the screened frames were replaced and control obtained by means of baited traps. Squirrel damage was restricted to the timbered areas as these rodents were never found at the open-station quadrats, although they were located less than 300 feet from a pine stand.

During the summer, evidence of insect defoliation was observed on various occasions. In a few instances, the larvae were observed feeding on the plants but more frequently the character of the injury indicated that it was caused by insects. Insects caused 5 and 1 percent, respectively, of the losses on litter and mineral quadrats in full shade. In 1933, all losses on litter and 15 percent on mineral surface at the part-shade station were caused by insects. During this season, no evidence of insect injury was noted at the open station. The larvae observed feeding on seedlings were not identified.

The percentage values of losses by various biotic agencies are shown in Table 21.

Soil fungi caused damping-off losses at the complete-canopy and part-canopy stations. This agency was responsible for 16 and 6 percent, respectively, of the total losses on litter and mineral surface quadrats at the complete-canopy station and 24 percent on the mineral surface quadrats only at the part-canopy station. No losses from this source occurred at the open station. Damping-off losses are increased by shade, high humidity and abundant soil moisture. These conditions prevailed more frequently in full shade than at the other stations. As a result, increased exposure at the cutover stations greatly reduced the occurrence of losses from damping-off. Moreover, the seedlings remained in a succulent condition for a longer period in heavy shade and consequently were susceptible to fungus attack for a longer period. Damping-off injury was most severe in the densely stocked plots, but did not become as serious at any time during the season as is frequently noted in coniferous seedbeds.

SEEDLING GROWTH AND LOSSES IN 1934

In the second season, weather instruments were established and observations of the quadrats begun May 15. A few days later the first seedlings appeared. Germination began somewhat earlier on the mineral-surface quadrats than on the litter. More uniform moisture under full shade provided conditions which caused an increase in the rate of germination on the timbered areas over that in the open. As in 1933, the litter surface was inferior to mineral soil for prompt germination of white pine seed. This unfavorable effect of litter was most pronounced in the open where very few seed germinated on litter and was least serious as an inhibiting factor under full shade. The influence of litter is reflected in the comparative germination numbers for the two surface mediums as presented in Table 22. According to the statistical test as presented in Table 35, only a moderate degree of difference existed between litter and mineral surfaces at the full canopy station and a pronounced degree of difference between these two surface types at the other stations. This difference was more pronounced at the cutover stations. In the open, where litter proved to be a critical factor in germination, only 57 plants appeared on the five litter quadrats in contrast to 2,199 plants on the same number of mineral quadrats. On the timbered areas where surface drying was less rapid, there was less difference between the amount of germination on litter and mineral surfaces.

In 1934, the principal physical killing agencies were the same as those noted during the previous season; namely, high surface temperatures and drought. Observation showed that available soil moisture was above the wilting coefficient in the surface soil during most of this growing season.

TABLE 22. GERMINATION BY MONTHS FOR 2 SURFACE TYPES AT 3 STATIONS IN 1934*

Month	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)	
	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface
May	—	2,101	—	160	—	557
June	2,601	1,865	346	1,819	38	1,204
July	900	235	56	537	19	430
August	26	4	28	31	—	8
September	—	—	—	—	—	—
Total	3,527	4,205	430	2,547	57	2,199

*5 quadrats for each surface type.

Nevertheless, soil moisture became limiting for seedlings at the two timbered stations during the last half of July. Following this period, surface-soil moisture was adequate throughout the remainder of the season. Open-grown seedlings suffered less from drought than the seedlings grown on timbered areas. At the open station, the soil was more compact and the absence of timber, which necessarily requires a large amount of moisture during the growing period, was undoubtedly a favorable factor in conserving soil moisture. Moreover, the roots of open-grown seedlings developed vigorously thereby maintaining contact with moist soil as desiccation occurred near the surface.

Drought was the most important single cause of loss at the full-canopy station. At this station, approximately 55 percent of seedling losses on litter and 47 percent of those on the mineral soil were attributed to this factor. At the part-canopy station, 5 percent of the losses on litter quadrats and 34 percent of deaths on mineral quadrats were caused by drought. At the open station, only 7 percent of the losses for the season were due to inadequate soil moisture. Drought loss in open was influenced by late germination of some seed which produced small plants that were affected more by mid-summer drought than the plants which became established early in the season. Table 36 shows that a moderate degree of difference existed in drought losses between litter and mineral surfaces at the full-shade station, but no significant difference in drought losses was noted between surfaces at the part-shade station.

Killing surface temperatures occurred only at the part-shade and full-sun stations. As previously noted, the part-shade quadrats were located in a more open portion of the stand than in 1933. As a result, the percentage of heat losses under part shade was higher than for the previous year. At this station, 89 percent of the losses on litter and 63 percent of those on mineral surface were caused by excessive insolation. As in 1933, high-surface temperature was the major killing agency in the open. All plants on

the litter quadrats were killed by heat and 61 percent of those on mineral surface were destroyed by this agency. Despite the very favorable moisture conditions during the season there were many days in May, June, and July when surface temperatures were well above the values known to be critical for young seedlings. The differences between heat losses on litter and mineral surfaces and between stations are given in Table 36. No significant difference occurred in heat losses between the two surface types at the part-shade station, but a significant difference in the effect of surface on heat mortality was observed at the open station.

TABLE 23. COMPARATIVE SEASONAL LOSSES BY AGENCIES (IN PERCENTAGE OF TOTAL LOSS) FOR 2 SURFACE TYPES AT 3 STATIONS IN 1934*

Agency	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)	
	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface
Heat	—	—	89	63	100	92
Drought	55	47	5	34	—	7
Insects	8	5	3	1	—	1
Fungi	37	48	3	1	—	—
Losses in percentage of germination	13	40	42	16	100	61

*Rodent losses were not included in computing percentage of loss by different agencies.

The rodents found to be active in the destruction of seed and plants were red squirrels, chipmunks, northern white-footed mice and domestic mice. The method used in protecting the quadrats from rodent damage has been previously described. Because of the careful attention given to their control, rodent activities were not typical of what might be anticipated under conditions of natural seeding. The greatest rodent damage occurred on the full-timbered area, where red squirrels invaded the quadrats several times in searching for ungerminated seed. Mice also destroyed a number of seedlings in digging up seed at various times during the season. In 1934, rodents destroyed 1,240 seedlings at the full-canopy station, 101 at the part-canopy station and 71 in the open. The principal losses on the full-timbered area were caused by squirrels. During the 1934 season, 6 squirrels and 1 northern white-footed mouse were caught in traps at the full-timbered station. In addition, 5 domestic mice were trapped at the part-timbered station and 2 domestic mice in the open.

The insect injury observed in 1934 was similar to that which occurred the previous season. Caterpillars defoliated a number of seedlings at all 3 stations but losses by this agency were greatest at the full-canopy station.

MISCELLANEOUS STUDIES

PHYTOMETER MEASUREMENTS

In 1934, a series of sunflower phytometers were installed at the 3 habitats under study in order to determine the direct effect of site conditions on the development of a rapidly growing species which would reach maturity in a single season. Phytometers have been reported by Clements and Goldsmith (1924) to give useful data in studies of the comparison of habitat conditions.

Five sunflower phytometers, which had been transplanted in individual containers, were sealed with water-tight covers and transferred to each of the three field stations. Optimum moisture conditions, for the soil in use, had been previously determined. The required amount of water was added when the phytometers were installed and transpirational losses replaced at 5-day intervals. The full-shade plants were tall and weak-stemmed in contrast to the vigorous individuals in part shade and full sun. At the end of the season the oven-dry weights of the plants were determined. Comparative weights and percentage relationships of dry material produced at each station are presented in Table 24. Although the plants in the open were somewhat

TABLE 24. AVERAGE DRY WEIGHT OF PHYTOMETER PLANT MATERIAL FOR 3 STATIONS

Plant	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)	
	Average (grams)	Dry weight (percent)	Average (grams)	Dry weight (percent)	Average (grams)	Dry weight (percent)
Top	1.96	24.2	7.14	88.3	8.09	100
Root	0.13	2.5	2.19	42.7	5.13	100
Total	2.09	15.1	9.33	64.0	13.22	100

TABLE 25. COMPARATIVE TRANSPIRATION RATES BY 5-DAY PERIODS FOR SUNFLOWER PHYTOMETERS AT 3 STATIONS IN 1934

Date	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)	
	Water loss*		Water loss**		Water loss**	
	Milliliters	Percent	Milliliters	Percent	Milliliters	Percent
July 25	219	50	308	71	436	100
30	13	7	177	98	180	100
August 4	144	31	409	89	458	100
9	134	38	320	91	353	100
14	158	36	444	101	441	100
19	89	25	229	65	350	100
24	134	39	378	110	344	100
30	132	41	295	93	318	100
Seasonal mean	128	40	320	89	360	100

*Mean transpirational loss for 4 phytometers.
**Mean transpirational loss for 5 phytometers.

restricted by insufficient soil space in the containers, as shown by the root-bound conditions existing when the experiment was completed, the amount of plant material produced at the 3 stations indicates that the factors affecting the phytometers may be similar to those influencing the development of seedlings at the 3 stations. As soil and water conditions were comparable for all phytometers, the difference in growth was apparently caused chiefly by differences in solar radiation at the 3 stations.

In general, transpiration rates for the 3 stations, as shown in Table 25, are in good agreement with the amount of exposure to which the plants were subjected. The difference in transpiration between the part-shade and open stations was less than expected probably on account of insufficient root space for the open-grown plants.

SECOND SEASON SURVIVAL

Limited data were obtained concerning second-season survival of the quadrats sown in 1933. Late in the summer of 1934, all live seedlings that had germinated the previous season and survived 2 seasons on the 3 study areas were counted. No attempt was made to follow periodic losses through the second season or to determine the causal agencies active in second season mortality. Second-season survival percentages by stations were found to be highest in part shade, with 73 and 71 percent living plants on litter and mineral surfaces, respectively (Table 26). Approximately 49 percent of the original seedlings were alive on mineral soil in the open, compared with complete loss on litter quadrats. In full shade, a larger percentage of plants survived than had been anticipated considering the poor initial growth they had made the first season. Despite the stunted condition of the full-shade plants, 31 and 34 percent respectively survived on litter and mineral-surface quadrats. The second-season growth of seedlings in full shade was very meager as shown by weights of dry material presented in Table 29. On

TABLE 26. FIRST AND SECOND SEASON SURVIVAL FOR QUADRATS SOWN IN 1933

Station and surface	First Season Survival		Second Season Survival	
	Number	Percent	Number	Percent
1. Complete canopy*				
Litter	798	59	418	31
Mineral	2,621	74	1,180	34
2. Partial canopy**				
Litter	99	85	85	73
Mineral	479	84	405	71
3. Open*				
Litter	1	6	—	0
Mineral	1,198	71	960	49

*3 fall-sown quadrats for each surface type.
**4 spring-sown quadrats for each surface type.

a dry-weight basis, two-year seedlings at the complete-canopy station averaged 8 percent as large as those in the open; whereas those from the part-shade quadrats were 34.5 percent as large as those at the open station. The remarkable ability of white pine seedlings to survive for two seasons under unfavorable growing conditions in heavy shade is in agreement with results obtained by Pearson (1930) in a study of western yellow pine seedlings.

Two-year-old seedlings on both the part-shade and open areas grew vigorously and appeared thrifty in every respect. Part-shade plants, however, were appreciably smaller than those on full-sun quadrats.

DISCUSSION OF RESULTS

Weather conditions for the two seasons differed chiefly only in the distribution of rainfall. The 1933 season was severe for young seedlings because of the extended drought period in early summer. An excess of precipitation in April provided adequate moisture for early season germination, but May, June, and July were deficient in the total amount of rainfall. During this period, rainfall came in light showers which were intercepted in a large measure by the canopy and litter at the timbered stations. The deficiency in rainfall resulted in a reduction in moisture in the surface soil resulting in hazardous conditions for the young seedlings.

Seasonal records showed a pronounced difference in site conditions at the 3 stations as influenced by the amount of exposure. The most significant of these factors affecting seedling development were radiation, surface temperature, soil temperature, and soil moisture. Differences in station conditions were directly reflected in germination as shown in Table 27.

TABLE 27. GERMINATION FOR 2 SURFACE TYPES AT 3 STATIONS IN 1933 AND 1934

Season	STATION 1 (complete canopy)		STATION 2 (partial canopy)		STATION 3 (open)	
	Litter surface	Mineral surface	Litter surface	Mineral surface	Litter surface	Mineral surface
1933	1,360*	3,395*	116**	570**	16*	1,959*
1934***	3,527	4,205	430	2,547	57	2,199
Total	4,887	7,600	546	3,117	73	4,158
Quadrat average	611	950	61	346	9	560

*Total for 3 quadrats.
**Total for 4 quadrats.
***Total for 5 quadrats.

Lack of agreement in the amount of germination for the two seasons was not considered significant because of possible differences in quality of seed and other uncontrollable factors. Furthermore, germination results at the part-shade station were not strictly comparable with those at the other two

stations in 1933 since these quadrats were spring-sown in contrast to fall seeding in the open and in full shade. In 1934, all quadrats were fall-sown. Consequently seedling numbers at the 3 stations were comparable and were also considered to be representative of differences of habitat conditions at the areas under study. Germination was favored at the timbered station through the protective influence of the canopy in maintaining more uniform surface moisture conditions. Under the canopy, seedlings continued to appear later in the season after germination in the open had ceased because of drier surface conditions at that station.

The canopy at the full-shade station was effective in diminishing the radiation available for plant seedlings far below the intensity in the open. Here the average value of light intensity for the two seasons was between 6 and 7 percent of full sunlight. The direct influence of weak light was clearly apparent through its effect in reducing seedling growth at this station. Following germination, seedlings developed very slowly in respect to both top and root growth. It was also noted that although a large proportion of these plants remained alive through the second season, there was very little increase in growth over that of the first year.

TABLE 28. COMPARATIVE SEASONAL LIGHT VALUES IN PERCENTAGE OBTAINED BY PAIRED BLACK AND WHITE ATMOMETERS

Season	STATION 1 (complete canopy)	STATION 2 (partial canopy)	STATION 3 (open)
1933	6.26	22.11	100
1934....................	6.94	43.11	100

At the part-shade station, one-year seedlings were 41 percent as large as those in the open and 34 percent as large at the end of two years. Although somewhat smaller than open-grown seedlings, these seedlings were normal both in respect to shoot and root development. The vigor of these plants is further indicated by the relatively high survival at the end of the second season as shown in Table 26.

At the full-sun station, the seedlings which escaped injury from high-surface temperatures showed excellent development. If the dry weight of plant material produced is adopted as a basis of comparison at the 3 stations, it becomes apparent that the growth rate is almost directly proportional to the amount of radiation available. Evidently where other factors are favorable, young white pine seedlings are capable of utilizing practically full sunlight under natural conditions existing in this region. This ability of pine to thrive so vigorously in the open very likely explains the excellent development of this species when seeded in open fields and abandoned pastures. Comparative dry weight relationships of plants at the 3 stations are presented in Table 29.

TABLE 29. OVEN-DRY WEIGHT OF FIRST AND SECOND SEASON SEEDLINGS FOR 3 STATIONS

Station	1-YEAR-OLD SEEDLINGS		2-YEAR-OLD SEEDLINGS	
	Oven dry weight		Oven dry weight	
	Grams	Percent*	Grams	Percent*
1. Complete canopy	0.0287	14.8	0.0545	8.0
2. Partial canopy	0.0804	41.5	0.2353	34.5
3. Open	0.1937	100.0	0.6812	100.0

*Based on weight of open-grown seedlings.

HEAT LOSSES

In addition to the influence of the site on seedling development, consideration must be given to the various factors responsible for seedling losses. Toumey and Neethling (1924) demonstrated that high surface soil temperature was a major factor in the mortality of coniferous seedlings in this region. They found that when surface temperatures exceed 122 degrees heat lesions are likely to develop on small white pine seedlings. Insolation at the soil surface was found to be critical for young seedlings in the open and on exposed portions of the part-shade area. High-surface temperatures were responsible for heat lesions which resulted in the death of 7 percent of the seedlings in part shade the first season and 12 percent the second season. Losses from high insolation were most severe in the open where temperatures in excess of 135 degrees F. occurred frequently. Here high-surface temperatures were responsible for some 39 percent of all plant deaths in 1933 and 53 percent in 1934. Because of the susceptibility of recently germinated seedlings to heat lesions, high-surface temperatures were found to be the most critical agency in mortality of seedlings in the open. No heat losses occurred either season in full shade.

Natural pine litter was definitely more hazardous as a surface medium than mineral soil in the early mortality of young seedlings. Critical temperatures occurred more days on litter than on mineral surfaces and all seedlings germinating on litter in the open were killed by heat before the close of the second season. On mineral soil, lethal temperatures were recorded only after the surface moisture became depleted through evaporation. Because of the better retention of moisture in mineral soil, a large proportion of

TABLE 30. SEEDLING LOSSES BY CAUSAL AGENCIES FOR BOTH GROWING SEASONS IN PERCENTAGE OF GERMINATION

Season	Heat	Drought	Rodents	Insects	Fungi
1933	11.1	12.8	5.9	0.6	1.7
1934	12.2	5.5	11.2	0.7	3.3
Average	11.6	8.0	9.1	0.6	2.6

the young plants survived the early succulent stage until stem tissue hardened resulting in immunity to late season high temperatures.

DROUGHT LOSSES

Several factors affect the availability of soil moisture for seedlings growing under forest conditions. Aside from the amount of precipitation, these include the competition of other vegetation, interception by canopies, the influence of litter and the lack of uniformity in the soil. Furthermore, the rate of root growth is significant in young seedlings as it may determine their ability to penetrate to deeper moisture as the surface zone becomes dry during periods of drought. In this study, drought conditions prevailed when the surface soil was reduced to the wilting coefficient in the zone occupied by seedling roots. Some 12.8 percent of all plants were killed by drought in 1933 and 5.5 percent in 1934.

RODENT LOSSES

The information regarding the activities of rodents in destroying seed and seedlings was obtained incidental to the investigation of physical site factors. In the original plans, no provisions were made to determine the extent of damage by rodents since they were excluded from the seeded quadrats in so far as possible. The various rodents found molesting the study plots were red squirrels, chipmunks and mice. Rodents were controlled by means of baited traps whenever evidence of their presence was observed on the study area.

Losses from rodent damage were greatest at the full-timbered station where red squirrels visited the quadrats a number of times and destroyed seedlings in searching for ungerminated seed. Damage by chipmunks and mice was most serious at the part-canopy and open stations. Rodents destroyed approximately 6 percent of all seedlings in 1933 and 11 percent in 1934. They were also responsible for the destruction of a limited amount of ungerminated seed. Apparently, the animals found to be destructive at these stations normally feed on pine seed when it is available and observations have shown that in this region squirrels destroy a large part of the seed when only a light crop is produced.

INSECT LOSSES

Only limited data were obtained on insect damage to the seedlings under observation. In only a few instances were the insects seen feeding on the plants. These were larvae and were not identified because facilities were not available for preserving the specimens in preparation for sending them to the laboratory. The greater part of the insect damage consisted in defoliation of the seedlings at the timbered stations. The heaviest loss occurred in part shade where 4 percent of the losses in 1933 were attributed to this agency. During the two seasons, less than 1 percent of all seedlings were killed by

insects. The limited amount of data obtained in this study suggests that insect damage in this region is not a major factor in first-season survival.

FUNGOUS LOSSES

Damping-off losses were confined to the two stations with overhead shade.[5] In the open, there were no losses from this cause during either season of study. The heaviest losses from this agency occurred at the full-shade station where 5.5 percent of the seedlings were killed in 1933 and 1.9 percent in 1934. At the part-shade station, losses were not as great as in full shade. Here 2.8 percent of the seedlings were killed by fungi in 1933 and 0.3 percent in 1934. It is apparent that heavy shade contributes to the damping-off losses. Evidently low light and high relative humidity under these conditions are favorable for the activity of damping-off organisms. Furthermore, the heavy shade retarded seedling growth thereby causing the seedlings to remain in a succulent condition for a longer period. Although the death of these seedlings should be directly attributed to damping-off, the heavy shade is an important contributing factor under natural conditions. As damping-off fungi were most injurious in full shade and were not a factor in mortality at the open station, it appears that this factor is not of major importance in the mortality of seedlings growing on clearcut sites or in the open stands in this region.

SUMMARY

In the autumn of 1932, 3 stations were established within the natural white pine type in the Yale Demonstration and Research Forest near Keene, New Hampshire for the purpose of studying the site factors influencing the early development and losses of eastern white pine (*Pinus strobus* L.). The stations were located within one half mile of each other on sites differing chiefly in the character of the overwood. Station 1 was established in a dense irregular-aged pure white pine stand; station 2 in a cutover stand in the 41 to 60 year age class in which approximately one third of the trees were removed in a logging operation in the winter of 1931-1932. Station 3 was located on a cutover area which formerly had been covered with a stand of pine containing a light admixture of hemlock and hardwoods. Determinations of air temperature, wind velocity, relative humidity, surface temperature, soil temperature, and soil moisture, light intensity, and evaporation were obtained for two growing seasons at the 3 study habitats. At each station, a number of quadrats representing two surface conditions, natural litter and mineral soil, were sown with equal quantities of white pine seed. When germination began, daily records were kept of the number of seedlings and mortality classified by causal agencies. The number of seedlings surviving at the end of the second season were also determined for the quadrats sown in 1933.

[5] Infected seedlings were examined by Dr. J. S. Boyce of Yale University.

The physical factors influencing seedling growth were directly affected by the degree of exposure at the 3 stations. The most important of these factors were solar radiation, surface temperature, soil temperature, and soil moisture. The average light intensity for the two seasons at the full-canopy station was about 7 percent of full sunlight. At the part-canopy station, radiation was approximately 22 percent in 1933 and 43 percent in 1934 of that in the open on clear days.

One of the most pronounced effects of the canopy was the reduction in surface temperatures at the timbered stations. On litter-surface quadrats, no surface temperatures above 120 degrees F. were recorded at the full-shade station during the two seasons. Greater exposure at the part-canopy station resulted in 17 days with surface temperatures above 120 degrees F. and 4 days that exceeded 135 degrees F. In the open, critical temperatures were more common. Records on litter surface for the two seasons showed 131 days with temperatures of 120 degrees F. or above and 82 days on which the maximum reached or exceeded 135 degrees F. At this station, critical temperatures were more common both seasons on litter surface than on the exposed mineral soil.

The shading effect of the canopy resulted in a reduction of soil temperature at a depth of 2 inches at the timbered stations. The mean soil temperature was lowered about 2.5 degrees F. at the part-shade station and 8 degrees F. at the full-shade station.

Weekly soil moisture determinations showed that during dry periods available moisture in the upper 3 inches of soil was lowest at the full-canopy station. Here available water was below the wilting coefficient for several weeks during the summer. Moisture conditions were somewhat better at the part-canopy station where the wilting stage existed for only short periods. At the clear-cut station, soil moisture in the upper three inches remained above the wilting coefficient throughout both growing seasons.

Due to its shading effect, the canopy tended to produce more favorable conditions for germination than the more exposed surface in the open. In general, high evaporation in the open restricted germination to a short period at the beginning of the growing season. However, under the full canopy, seed continued to germinate during rainy periods throughout the summer. The comparative germination figures per quadrat in 1934 were 773 seedlings in full shade, 298 in part shade and 227 in the open.

In comparing germination on litter and mineral surfaces, an advantage is noted in favor of the mineral surface. This influence was least important in full shade and most pronounced in full sun at the open station where an average of nine seedlings per quadrat appeared on litter in contrast with 560 on the exposed mineral surface.

Seedling development was definitely restricted by the overhead canopy at the timbered stations. One-year seedlings grown in full shade were about

15 percent as large as those in the open when compared on a basis of dry weight. Plants in part shade were approximately 41 percent as large as those in the open.

The major influence of the canopy in affecting seedling survival was in the reduction of radiation intensity. Although a large proportion of the seedlings in full shade received sufficient light for survival through both growing seasons, inadequate radiation lowered plant vigor so seriously that their chances of ultimate survival were seriously reduced. Seedlings in part shade were smaller than those in full sun but were otherwise vigorous and well developed in respect to the shoot-root ratio. The vigorous seedling development in the open indicated that when other factors were favorable, white pine seedlings increased in growth rate in direct proportion to the amount of radiation available in this region.

High surface temperatures were a major factor in mortality at the part-shade and full-sun stations, but no heat damage was noted at the full-canopy station. At the part-shade station, 10.8 percent of the plants were killed by heat and 46.6 percent in the open. This factor was the major single agency in mortality in the open.

Drought was responsible for the death of 11.4 percent of all seedlings in full shade, 3.3 percent in part shade and 2.1 percent in the open.

Rodents were the major biotic factor in mortality. They destroyed 13.3 percent of the plants in full shade, 3.1 percent in part shade and 1.8 per cent in full sun.

Insect injury was not a major factor in seedling mortality at the 3 areas under study. Fungi were responsible for 4.0 percent of the seedling losses in full shade and 0.7 percent in part shade. No losses were caused by this factor in the open.

CONCLUSIONS

1. Overhead canopy of pine stands improved conditions for seedling germination through its effect in reducing evaporation from the surface soil. Lower soil temperature in the shade early in the spring retarded the initiation of germination a few days. This effect, however, is not considered to be significant in ultimate seedling development.

2. Natural pine litter acts as an unfavorable medium for the germination of white pine seed under the conditions studied. Because of the porous character of litter it does not retain moisture as well as mineral soil. This unfavorable effect of litter was least important under a full canopy where it reduced germination to about two thirds of that on mineral soil. In the open where drying conditions were more severe only 73 seedlings occurred on litter quadrats compared with more than 4,200 on mineral surface.

3. Excessive surface temperature was a major factor in seedling mortality wherever the plants were exposed to direct insolation. This was the

most important killing agency in the open. In was less severe in part shade and did not become critical either season for seedlings under the complete canopy.

4. Soil moisture conditions in the zone occupied by the roots of first-year seedlings were most critical under the full canopy. Drought periods were shorter at the part-canopy station and did not become a serious factor in the open where other vegetation was eliminated.

5. Drought in the forest was augmented by the interception of rainfall by the canopy and by pine litter. In a dense pine stand, as much as one half inch of precipitation may be intercepted by the canopy and heavy litter. Drought losses in the shade were increased through the influence of low radiation in reducing seedling vigor with consequent weak root development.

6. Light was not reduced too low under the full canopy to prevent white pine seedlings from surviving for two growing seasons. Nevertheless, it was inadequate to support vigorous growth. Consequently, low light resulted in inferior plants which suffered heavy mortality the first season and showed little promise of permanent establishment.

The results of this investigation show that in this region approximately 20 percent of full sunlight is required for satisfactory first year seedling growth. Plants grown in full sunlight were larger and more vigorous than those in part shade.

7. In this region, red squirrels, chipmunks, and mice are likely to destroy an appreciable amount of white pine seed and seedlings under natural forest conditions.

8. Insects do not appear to be a major factor in the first season survival of white pine seedlings.

9. The records of damping-off mortality indicate that under natural conditions losses by this agency are important only in weak plants growing in heavy shade.

Comparison of Factors Influencing the Early Establishment of Western White Pine and Eastern White Pine

It is interesting to note the major factors found significant in the investigations of western white pine by Haig (1936) and in the present study. In both studies, the major causes of seedling losses were damping-off organisms, insects, surface soil temperature, deficient soil moisture, and rodents. In both sets of experiments, rodents were excluded whenever possible.

Damping-off fungi were a major agency in mortality in Idaho, but were only of minor importance in New Hampshire. This difference may be attributed in part to greater alkalinity in western soils.

In both investigations, damping-off fungi were most serious in full shade and on litter surfaces.

High surface temperature and drought were the most important physical agencies in mortality in both regions. An agreement was noted in that surface temperatures were most severe on cutover areas and drought losses were heaviest in full shade.

Low radiation under full shade was not a direct factor in mortality in either region. It was, however, a contributing factor through its effect in retarding root growth which resulted in greater drought losses in full shade during dry periods. Both investigations revealed that insolation losses were definitely higher on litter surface than on mineral surface.

Drought losses for both the western and the eastern species were greatest at the full-shade stations. In comparing the effect of drought at the other stations, Haig (1936) noted greater drought damage in full sun than in part shade. In the experiment with eastern white pine, drought losses were least at the full-sun stations. This may be attributed to the fact that the western stations received a much smaller amount of summer precipitation than the New Hampshire stations.

APPLICATION OF RESULTS IN SILVICULTURAL PRACTICE

The results of this investigation have a direct relation to the silvicultural treatment of white pine stands in which the objective of management is to obtain a high proportion of pine by natural methods of regeneration after logging. The recommendations will apply especially to the production of pine on the lighter soils in central New England. White pine is better adapted to the sandy soils and therefore it competes more successfully with hardwoods on soils of this character.

Although pine seed will germinate most completely in full shade, the seedlings obtained are too weak at the end of the first season to develop as permanent reproduction. Reducing the stand density by thinning operations will improve conditions for seedling growth, but ultimate survival is likely to be low unless greater exposure of the surface is obtained than that usually provided in such cuttings. In stands that are evenaged in character, plans should be made to obtain reproduction near the end of the rotation. This would involve a shelterwood cutting in which the mature stand is removed in two cuttings. In the first of these operations, approximately 40 to 60 percent of the soil surface should be exposed. The residual stand will provide ample seed for reproduction, retard desiccation of the surface soil during the germination period, prevent excessive losses from high surface temperature, yet permit sufficient light to reach the forest floor to support vigorous seedling growth. It is suggested that the residual stand be removed after reproduction has become established and is no longer subject to injury from exposure to full sunlight. The period required between cuttings will depend largely upon seed production and the condition of the surface soil in its

ability to support germination. In this region, many of the second-growth pine stands have developed as groups with each group representing one age class. The small groups can be harvested to the best advantage by clear cutting. The opening made by this method of cutting may be regenerated by seed from adjacent trees. Partial protection may also be provided for the area by the adjacent immature pine.

After cutting, it will usually be necessary to dispose of the brush by lopping and scattering. Unless the litter is disturbed sufficiently in logging to expose the mineral soil, it should be broken up later preferably just prior to maturity of a seed crop. Usually considerable hardwood reproduction is present in mature pine stands. This growth should be cut back at the time the seed cutting is made in order to reduce competition for soil moisture and also to improve light conditions. Full consideration should be given to market conditions as this will be a dominant factor in determining the time of harvesting.

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APPENDIX

STATISTICAL ANALYSES

The statistical analyses, as presented in Tables 31 to 34, consisted in determining significant variance in physical factors at the 3 stations, differences in germination, in heat losses, and in drought losses. The method proposed by Fisher (1936) was used to test significance between means. The various constants were calculated and the degree of significance indicated. A high degree of significance shows that a real difference exists in the intensity of two factors.

TABLE 31. STATISTICAL CONSTANTS FOR VARIOUS SITE FACTORS IN 1933.

Source of variance	Degrees of freedom	Mean difference	Sum of deviations squared	Values for (t)	Probability standards 0.05–0.01	Significance
Atmometers						
Black less white						
Stations 1 and 2...	3	1.29	0.6615	5.510	3.182–5.841	Medium
Stations 2 and 3...	3	6.34	2.1427	14.998	3.182–5.841	High
Stations 1 and 3...	3	7.63	4.7966	12.073	3.182–5.841	High
Atmometers Black						
Stations 1 and 2...	3	3.27	7.2623	4.203	3.182–5.841	Medium
Stations 2 and 3...	3	13.44	19.3149	10.599	3.182–5.841	High
Stations 1 and 3...	3	16.71	47.8196	8.380	3.182–5.841	High
Atmometers White						
Stations 1 and 2...	3	1.82	4.1186	3.106	3.182–5.841	Medium
Stations 2 and 3...	3	7.10	8.8530	8.266	3.182–5.841	High
Stations 1 and 3...	3	9.33	18.8626	7.871	3.182–5.841	High
Soil temperature (litter surface)						
Stations 1 and 2...	3	0.25	2.9400	1.780	3.182–5.841	None
Stations 2 and 3...	3	6.28	8.4688	7.476	3.182–5.841	High
Stations 1 and 3...	3	6.02	2.4076	13.260	3.182–5.841	High
Soil temperature (mineral surface)						
Stations 1 and 2...	3	2.30	8.9900	2.659	3.182–5.841	None
Stations 2 and 3...	3	7.17	16.2533	6.143	3.182–5.841	High
Stations 1 and 3...	3	8.37	8.9961	9.682	3.182–5.841	High
Soil temperature (litter and mineral)						
Station 1.........	3	1.92	7.5181	2.434	3.182–5.841	None
Station 2.........	3	2.52	0.2636	17.001	3.182–5.841	High
Station 3.........	3	3.42	5.7874	4.935	3.182–5.841	Medium
Maximum soil temperature (litter surface)						
Stations 1 and 2...	3	0.67	0.8674	2.519	3.182–5.841	None
Stations 2 and 3...	3	12.90	27.5000	8.520	3.182–5.841	High
Stations 1 and 3...	3	12.87	41.3233	6.937	3.182–5.841	High
Maximum soil temperature (mineral surface)						
Stations 2 and 3...	3	13.50	56.0600	6.246	3.182–5.841	High
Maximum soil temperature (litter and mineral)						
Station 2...........	3	6.00	6.3400	8.255	3.182–5.841	High
Station 3........	3	6.57	0.2474	45.820	3.182–5.841	High

In 1933, light intensity determinations, as expressed by the difference in water loss from atmometers, were significantly different at the 3 stations. This difference in radiation brought about a distinct variation in seedling development at the 3 stations.

Soil temperature values failed to show a real difference between full-shade and part-shade stations either on mineral or litter surface. These results indicate that soil temperature is not a major factor in causing a difference in seedling growth at these stations. However, at the part-shade and open stations, the mean soil temperatures showed a significant difference between stations. Moreover, at these stations, the soil temperature was affected by the type of surface.

Data are presented in Table 32 showing variance in germination on the 2 surface types and at different stations for the 1933 season. Germination on litter and mineral surface quadrats differed significantly at the full-shade station, but did not show a significant difference at the part-shade station. Station difference was not important when comparing stations 1 and 2 on litter surface quadrats. On the mineral quadrats, difference in station was a significant factor in comparing stations 1 and 2 as well as 1 and 3, but was not significant in comparing stations 2 and 3.

TABLE 32. STATISTICAL CONSTANTS FOR GERMINATION VALUES IN 1933.

Source of variance	Degrees of freedom	Mean difference	Sum of deviations squared	Values for (t)	Probability standards 0.05–0.01	Significance
Germination						
(litter and mineral)						
Station 1	3	683	165,606	4.110	3.182–5.841	Medium
Station 2	3	118	28,847	2.408	3.182–5.841	None
(litter surface)						
Stations 1 and 2	3	411	180,235	2.376	3.182–5.841	None
(mineral surface)						
Stations 1 and 2	3	939	132,798	6.315	3.182–5.841	High
Stations 2 and 3	3	444	251,594	2.168	3.182–5.841	None
Stations 1 and 3	3	481	53,144	5.111	3.182–5.841	Medium

TABLE 33. STATISTICAL CONSTANTS FOR HEAT AND DROUGHT LOSSES IN 1933.

Source of variance	Degrees of freedom	Mean difference	Sum of deviations squared	Values for (t)	Probability standards 0.05–0.01	Significance
Heat losses						
(litter and mineral)						
Station 3	3	221	44,408	2.570	3.182–5.841	None
Drought losses						
(litter and mineral)						
Station 1	3	197	36,181	2.537	3.182–5.841	None

TABLE 34. STATISTICAL CONSTANTS FOR VARIOUS SITE FACTORS IN 1934.

Source of variance	Degrees of freedom	Mean difference	Sum of deviations squared	Values for (t)	Probability standards 0.05–0.01	Significance
Atmometers						
Black less white						
Stations 1 and 2...	4	3.47	3.4107	8.41	2.776–4.604	High
Stations 2 and 3...	4	5.49	7.2886	9.09	2.776–4.604	High
Stations 1 and 3...	4	9.13	11.1799	12.22	2.776–4.604	High
Atmometers						
Black and white						
Station 1.........	4	0.68	1.8529	2.25	2.776–4.604	None
Station 2.........	4	4.16	4.0189	9.29	2.776–4.604	High
Station 3.........	4	9.65	11.8573	12.53	2.776–4.604	High
Atmometers black						
Stations 1 and 2...	4	6.14	4.3993	13.09	2.776–4.604	High
Stations 2 and 3...	4	10.46	50.1685	6.60	2.776–4.604	High
Stations 1 and 3...	4	16.83	40.9299	11.75	2.776–4.604	High
Atmometers white						
Stations 1 and 2...	4	2.69	2.9341	7.02	2.776–4.604	High
Stations 2 and 3...	4	4.98	23.7426	4.58	2.776–4.604	Medium
Stations 1 and 3...	4	7.65	11.7651	9.97	2.776–4.604	High
Soil temperature (litter and mineral)						
Station 1.........	4	0.58	0.5280	3.58	2.776–4.604	Medium
Station 2.........	4	0.68	0.9080	3.19	2.776–4.604	Medium
Station 3.........	4	1.06	1.1520	4.42	2.776–4.604	Medium
Soil temperature (litter)						
Stations 1 and 2...	4	1.72	2.1080	5.29	2.776–4.604	High
Stations 2 and 3...	4	6.02	4.2880	13.00	2.776–4.604	High
Stations 1 and 3...	4	7.42	2.1680	22.55	2.776–4.604	High
Soil temperature (mineral)						
Stations 1 and 2...	4	1.66	7.3900	2.73	2.776–4.604	None
Stations 2 and 3...	4	6.16	0.7320	32.25	2.776–4.604	High
Stations 1 and 3...	4	7.82	12.1480	10.04	2.776–4.604	High
Maximum soil temperature (mineral surface)						
Stations 1 and 2...	4	2.22	6.4680	3.91	2.776–4.604	Medium
Stations 2 and 3...	4	9.28	8.7880	13.99	2.776–4.604	High
Stations 1 and 3...	4	11.30	4.9600	22.69	2.776–4.604	High
Maximum soil temperature (litter surface)						
Stations 1 and 2...	4	1.70	0.7400	8.85	2.776–4.604	High
Stations 2 and 3...	4	11.00	0.9200	51.40	2.776–4.604	High
Stations 1 and 3...	4	12.66	0.7120	66.98	2.776–4.604	High
Maximum soil temperature (litter and mineral)						
Station 1.........	4	0.82	1.628	2.88	2.776–4.604	Medium
Station 2.........	4	1.30	1.040	5.70	2.776–4.604	High
Station 3.........	4	0.62	1.708	2.12	2.776–4.604	None
Phytometers						
Stations 1 and 2...	7	192	31,843	8.07	2.306–3.355	High
Stations 2 and 3...	7	49	16,814	2.83	2.306–3.355	Medium
Stations 1 and 3...	7	232	17,385	13.18	2.306–3.355	High

TABLE 35. STATISTICAL CONSTANTS FOR GERMINATION VALUES IN 1934.

Source of variance	Degrees of freedom	Mean difference	Sum of deviations squared	Values for (t)	Probability standards 0.05–0.01	Significance
Germination						
(litter and mineral)						
Station 1.........	5	541	626,262	3.070	2.571–4.032	Medium
Station 2.........	5	423	98,076	6.043	2.571–4.032	High
Station 3.........	5	428	230,304	3.989	2.571–4.032	High
(litter surface)						
Stations 1 and 2...	5	1296	1,813,765	4.305	2.571–4.032	High
Stations 2 and 3...	5	75	8,268	3.695	2.571–4.032	Medium
Stations 1 and 3...	5	1370	1,754,452	4.628	2.571–4.032	High
(mineral surface)						
Stations 1 and 2...	5	822	646,636	4.592	2.571–4.032	High
Stations 2 and 3...	5	147	52,675	2.866	2.571–4.032	Medium
Stations 1 and 3...	5	942	1,366,449	3.604	2.571–4.032	Medium

In 1933, heat losses occurred at the open station only. It seems probable that the absence of a significant difference can be attributed to the fact that very few seedlings appeared on the litter quadrats.

In 1933, drought losses occurred at the full canopy station only. No statistical difference was found between the losses on litter and on mineral quadrats.

Differences in radiation intensity as measured by atmometers are shown in Table 33. Close agreement in the readings for both black and white spheres at station 1 emphasizes the low radiation intensity at this station.

Soil temperature data for this season varied significantly between stations. In comparing temperatures between litter and mineral surfaces, only a moderate difference was apparent at stations 1 and 2, but the temperatures differed greatly between the 2 surface types at the open station. It may be concluded from these results that the insulating effect of litter was more pronounced in full sun than at the timbered stations.

When water losses from phytometers at different stations are compared, it may be noted that a high degree of difference was evident between stations 1 and 2, but a much smaller difference between stations 2 and 3. This unexpected behavior may be attributed to insufficient root space in plant containers. This reduced plant growth somewhat by restricting root development of the plants at the open station. For this reason, the full effects of growing conditions in the open were not completely expressed by transpirational losses.

In 1934, germination figures are compared statistically for variance between surfaces and between stations in Table 35. The effect of surface was very significant at the part-shade and open stations and less pronounced at the full-shade station. In testing for the influence of habitat, a pronounced difference was noted between stations 1 and 2, stations 1 and 3, and to a lesser extent between stations 2 and 3. On litter surface, a pronounced dif-

TABLE 36. STATISTICAL CONSTANTS FOR HEAT AND DROUGHT LOSSES IN 1934.

Source of variance	Degrees of freedom	Mean difference	Sum of deviations squared	Values for (t)	Probability standards 0.05-0.01	Significance
Heat losses						
(litter and mineral)						
Station 2	5	8	202	2.391	2.571-4.032	None
Station 3	5	219	37,618	5.072	2.571-4.032	High
(litter surface)						
Stations 2 and 3	5	24	1,432	2.789	2.571-4.032	Medium
(mineral surface)						
Stations 2 and 3	5	203	50,654	4.042	2.571-4.032	Medium
Drought losses						
(litter and mineral)						
Station 1	5	33	2,619	2.912	2.571-4.032	Medium
Station 2	5	10	847	1.566	2.571-4.032	None
(litter surface)						
Stations 1 and 2	5	68	4,532	4.545	2.571-4.032	High
(mineral surface)						
Stations 1 and 2	5	25	2,396	2.283	2.571-4.032	None

ference was shown in comparing stations 1 and 2. Only a moderate difference was noted in making the other comparisons.

Statistical constants for heat and drought losses are presented in Table 36. Surface medium was not important in affecting heat losses at station 2 but was highly significant at station 3. A real difference between stations 2 and 3 was noted on both surface types.

In 1934, drought losses were important only at the full-shade and part-shade stations. Mortality by this agency was significantly higher on litter than mineral surface at the full-shade station, but no difference was apparent at the part-shade station. This factor was of greater importance on litter when comparing stations 1 and 2 than on mineral surface.

BIOTIC AND PHYSIOGRAPHIC SUCCESSION ON ABANDONED ERODED FARMLAND[1]

By

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[1] Based on a thesis submitted to the Faculty of the Graduate School of the University of Oklahoma in partial fulfillment of the requirements for the degree of Doctor of Philosophy, June, 1939. Contribution from the Zoological Laboratories, University of Oklahoma. No. 203 n.s.

CONTENTS

BIOTIC AND PHYSIOGRAPHIC SUCCESSION ON ABANDONED ERODED FARMLAND

INTRODUCTION

Central Oklahoma was opened to agricultural occupation April 22, 1889. Many of the settlers came from farming regions to the north where intensive agriculture was the rule. Prairieland was the first to be plowed because no preliminary clearing was necessary. Later some woodland was converted into farmland.

Climate, topography and parent material render the soils of this region especially susceptible to erosion by water. Not realizing this danger, farmers were slow to take steps to save their soil. In a few years erosion had taken a heavy toll of the fertility of the fields and abandonment of some damaged land had begun. Usually no treatment was given the soil to aid or hasten recovery. Such areas were allowed to lie idle or sometimes were used as pastureland. In some cases the fields were replowed after lying fallow for a few years. Usually these were soon abandoned because the soil had not recovered sufficiently to make cultivation profitable.

Data presented in this paper show that even after vegetation has occupied eroded farmland for some time, the soil has improved very little, since plants occupying it the first few years following abandonment are shallow rooted and short lived and their remains are soon oxidized.

Soil suited to agriculture in central Oklahoma was developed only under the influence of deep-rooted perennials as characterize the prairie. Many years are required to develop soil to a point where prairie vegetation can again occupy it. Very little land has been abandoned in central Oklahoma long enough for perennial grasses characteristic of the prairie to invade and become established. Examination of soil from areas longest abandoned shows a humus content about half that of a climax prairie.

Prairies of east central Oklahoma, with the exception of those on bottom land, show upon analysis a humus content too low to make cultivation feasible. Moderate grazing is the most practical use for the land. In the western part of the study area, humus and clay content of the soil is higher, and waterholding capacity greater, indicating soil that can be plowed, providing steps are taken to maintain the organic matter content of the soil and to prevent erosion.

According to reports of the Soil Conservation Service (McDonald 1938), Oklahoma has suffered as much erosion since agricultural occupation as some of the oldest farming districts of the United States although one of the last states to be settled. In recent years much has been done to curb erosion on areas which still possessed agricultural value. Terracing, contour and

strip farming and improved methods of tillage have decreased the annual toll from erosion.

This is the first study carried out in this region with the purpose of tracing the changes in plant and animal life and the corresponding soil developments as abandoned, eroded, farmland develops a covering of prairie vegetation. Such studies are necessary before procedures can be recommended to facilitate biotic and physiographic recovery.

The writer feels that the present work provides a basis for experimental procedure which will lead to development of methods of restoring abandoned, eroded land to a useful condition in as short a time as practical and utilizing the help of nature as much as possible. It is not the purpose of this work to devise methods and procedures to hasten recovery of eroded land but to study some of the interrelationships of the organisms involved in the natural process of recovery.

The writer wishes to thank Dr. A. O. Weese for suggesting the problem and directing the research, Dr. A. I. Ortenburger for aid with the work on mammals, Dr. Milton Hopkins for aid in checking the identity of specimens of plants, Dr. Melville Hatch of the University of Washington for identifying certain Coleoptera, and the University of Oklahoma for aid in the form of a research fellowship.

LITERATURE

Numerous studies have been made which dealt with various phases of the present work, although none have been carried out which treat directly with the problem under consideration. Since the mixed-grass prairie has been regarded as the climax to which all developmental stages studied are progressing, it is important to compare the results obtained by the writer with other similar studies on the prairie.

The autumnal animal communities of a prairie near Chickasha, Oklahoma, were studied by Smith and Shackleford (1928) who found the same species present in the fall communities as were found by the writer. Shackleford (1926) also studied the animal communities of an Illinois prairie, including some secondary successional stages. Among her conclusions the following is of particular significance in relation to the present study. "The most characteristic relationship between the secondary successional stages and the climax in 1926 was found in the fact that certain of the influent animals of the high prairie were taken in greater abundance in subseral stages than in the climax. The subseral stages were largely unbalanced approximations of the high prairie in which the bulk of the population consisted of relative disproportionate numbers of species also characteristic of the mature high prairie."

Isely (1937) has studied seasonal succession and soil relations of northeastern Texas acridians and found that in certain instances grasshopper suc-

cession is determined by specific food plants but chiefly is determined by interrelations resulting from vegetative cover and climate. Soils and their related vegetation used as food or shelter appear to be primary factors in determining local acridian communities and the micro-climate of specific habitats. As will be pointed out later in this paper, the writer found most species of grasshoppers to be associated with definite biotic communities.

After studying the activities and distribution of certain wild mice in relation to biotic communities in Illinois, Johnson (1926) concluded that the prairie deer mouse *(Peromyscus maniculatus bairdii)* is characteristically an inhabitant of open fields and that these mice must belong to some subclimax community rather than to the Andropogon climax since they were much more numerous in open fields and disturbed vegetation. It is true that the deer mouse is usually more abundant in seral communities yet they are more uniformly distributed throughout the prairie. It is not a question of an organism belonging to any particular community but of its behavior in different communities.

The writer found deer mice most abundant in pioneer stages of prairie succession but also present in small numbers in undisturbed prairie. Dice (1922) found in Riley County, Kansas, that these mice were most abundant on rocky ground, where grasses and sedges were absent. In some notes on mammals in Riley County, Kansas, he said

The mole *(Scalopus aquaticus)* is absent in upland prairie. The shrew, *Blarina brevicauda caroliniana* and the skunk are inhabitants of the prairie while the deer mouse is common on the prairie and on rocky ground. Pocket gophers are scarce on the high prairie but more numerous in the moist prairie. Pocket mice *(Perognathus)* inhabit ground with scant vegetation and rocky soil. Ground squirrels are common on prairie hills.

These statements are borne out by data presented in this paper. A study of the rodents of overgrazed and normal grassland in Cleveland and McClain counties, Oklahoma, was made by Phillips (1935). He found jackrabbits to be more numerous in moderately overgrazed pastures, cottontails more numerous in well-grassed areas, pocket gophers in subclimax vegetation where the soil is favorable, ground squirrels in mowed hayfields and deer mice in moderately overgrazed areas.

The writer failed to take deer mice in overgrazed areas, the greatest number being found in lightly grazed areas. At the time this study was made (1938), the cotton rat *(Sigmodon hispidus texianus)* was more numerous than for a good many years previously.

Plant succession on abondoned eroded fields in southeastern Ohio has been studied by Larsen (1935) who found that after a number of years the most eroded portions of the fields had developed a weedy type of vegetation, consisting of goldenrods, asters, *Plantago lanceolata, Ambrosia artemisifolia, Rumex acetosa,* Canada blue grass, *Poa compressa, Daucus carota,* poverty

grass (*Danthonia spicata*), triple awn grass (*Aristida obligantha*) and yarrow, *Achillea millefolium*. On somewhat better soils, *Andropogon virginicus* and *Aristida obligantha* dominate the vegetation. *Agrostis alba* dominates less eroded soils and on the best soil Kentucky blue grass (*Poa pratensis*) comes in. Larsen's study did not trace changes in vegetation on eroded areas from year to year but merely gave the differences in vegetation on soils of different quality several years after abandonment.

The studies of Weaver and Fitzpatrick (1934) on the prairie, of Albertson (1937) on the mixed prairie of West Central Kansas, and of Harvey (1908) on floral succession in the prairie of South Dakota give clues as to certain universal features of the prairie and have enabled the writer to compare prairies of central Oklahoma with those of other parts of the Great Plains.

Clements (1916) stated that the widespread dominants of fallow fields of prairies and plains are Salsola and Helianthus, the latter represented by *H. annuus* in the eastern portion and *H. petiolaris* in the western. *Erigeron canadensis* is perhaps next in importance in fields while Grindelia, Gutierrezia and *Artemisia frigida*, though abundant, are of still greater importance in pastures.

Other indicators of abandoned fields listed by Clements are: *Euphorbia marginata, E. geyeri, Ambrosia artemisioefolia, Iva xanthifolia, Chenopodium album, Panicum oapillare, Eragrostes pectinacea, Cenchrus tribuloides (pauciflora).*

The relationship between animals and soils have been summarized by Taylor (1935). Grinnell (1923) discussed burrowing rodents of California as agents in soil formation while Byers, Kellogg, Anderson, and Sharp (1938) treated the role of living organisms in soil formation.

Microorganisms are of paramount importance in changes constantly occurring in the soil but it has been impossible to study them in the present work. The work of Starkey (1938) and Thom and Humfield (1932) provide us with valuable information as to the reciprocal effects of microorganism and higher plants.

Just what the combined effect of erosion and cropping would be on the organic content of soil has not been determined but some knowledge has been obtained concerning the effect of different cropping systems on the organic content of soil. The effect of crops and cropping systems upon organic carbon and nitrogen of soil was studied by Metzger (1936). He found that non-legume crops produced a decline over a period of years in nitrogen and carbon content but that a stability was being approached for each crop and cropping system.

Snyder (Waksman 1936) found that when prairies in Minnesota are brought under cultivation, humus decomposition sets in rapidly. After cultivation for some time, this soil contains less humus than prairie soil but the

rate of its decomposition is greatly reduced. Other workers on the same problem find that an equilibrium is eventually established for various types of crops.

Robinson (1932) discussed cases where soil showed a drop in organic content following cultivation. All evidence points to the fact that regardless of the effect of erosion, abandoned farmland will have a lower humus content than soil of climax prairie. No one knows how long it will take for the humus content to return to its original condition. Many factors are at work.

Cutler (1938) stated that the organic matter content of soil increases most rapidly under a grass cover. Plowing and tilling operations in the production of cultivated crops result in a continuous and fairly rapid reduction in the organic content of soil. Bradfield has shown that 40 years cropping on Nappanee soil in Paulding County, Ohio, has increased the weight per cubic foot in the first foot from 65.5 lbs. to 81.7 lbs.; pore space has declined from 60.3 to 50.5 percent, and organic matter from 132,000 lbs. per acre in virgin soil to 89,400 pounds in soil cropped for 40 years. Under many conditions erosion has a greater effect on productive capacity of soil than all other deteriorating processes combined.

In his chapter on "Soil Organic Matter and Soil Humus" in the United States Department of Agriculture Yearbook for 1938, Nikiforoff stated that the average content of humus in mature soil remains relatively constant as long as no change in natural conditions occurs. Any change in natural conditions that upsets the equilibrium will be followed by a corresponding change in humus content of the soil. Reestablishment of the old balance usually takes a much longer time than it did to accomplish the striking changes produced by artificial processes. Nikiforoff stated that the humus content of the A-horizon of prairie in Kansas, Nebraska, and the Dakotas varies from 5 to 10 percent. The average content of humus in every mature soil is in equilibrium with the environment.

The relation of certain inherent soil properties to soil erosion was studied by Lutz (1933) who found that erosiveness or nonerosiveness was due to the degree of aggregation of the finer fractions and their ease of dispersion in water. Soils with large and stable aggregates are relatively nonerosive.

Baver and Rhodes (1932) found that soils high in organic matter contain from 15 to 30 percent more granules than those low in organic matter and that these aggregates are three times more stable than those low in organic colloids. These results are added evidence that rate of erosion is affected by degree of aggregation of soil particles which in turn is due to a large extent to the amount of organic matter in the soil.

Soil aggregates are not composed of inorganic materials alone as was shown by Metzger and Hyde of Kansas (1938) who found that the more aggregated portion of the soil contained significantly more organic carbon than the less aggregated portions. They believed that these results lend weight

to the assignment of an important role to organic matter in the aggregation of mineral particles of soils. Tyulin (1938), a Russian worker, stated that organic matter of soil colloids consists of a fraction loosely held at the surface of gels and a more firmly united portion. The evaluation of the more loosely held humates may serve as a valuable criterion of soil fertility or of the extent to which soil may be cultivated. Stephenson (1938) working in Oregon found that the water-soluble portion of organic matter returned to the soil may be absorbed by soil colloids, organic and inorganic, and held against future plant needs. The greatest quantity of water-soluble nutrients was found in surface soil, where organic matter is the most abundant and biological processes are most active.

Bouyoucos (1935) suggested that the clay-sand ratio might be used as a criterion of susceptibility of soils to erosion. He studied soils of low and high degrees of erosibility and found a correlation between the clay ratio and resistance to erosion. Soils with a low clay ratio were found to be resistant to erosion and those with a high clay ratio easily eroded. Robinson (1932) discussed certain inherent characteristics of soils which affect their tendency to erode. Generally speaking, a granular or crumb structure favors resistance to erosion (as was pointed out by Lutz 1935) while a deflocculated or single grain structure renders soils liable to erosion. The presence of a high proportion of organic matter is helpful in diminishing liability of erosion.

THE REGION STUDIED

The areas chosen for study are distributed over four counties of central Oklahoma—McClain, Cleveland, Oklahoma, and Logan. It was desired to have study plots well scattered so that conclusions would not be based upon conditions purely local in character. Locations of the areas and the route traveled in this study are shown in Figure 1. The areas studied represent conditions found over an area of approximately 800 square miles. The route traveled is about 260 miles in length.

The eastern portion of the route passes through a region covered with soil belonging to the Hanceville-Conway group, the northern and western parts through a region occupied by the Zaneis-Renfrow soil group and the southern part traverses a region occupied by soils of the Windthorst-Nimrod group.

The Yearbook of Agriculture for 1938 contains a revised soils map of the United States. Most of McClain County and a portion of Cleveland County belong to the Windthorst-Nimrod group. Of these the Yearbook has to say:

> The Windthorst and Nimrod and associated soils occupy the West Cross Timbers section, an irregular north-south belt of rolling timbered land, extending from north central Texas to south central Oklahoma. Native vegetation chiefly post-oak and blackjack-oak, with some hickory and other trees. The parent material is the weathered residue of sandstone. The soils are

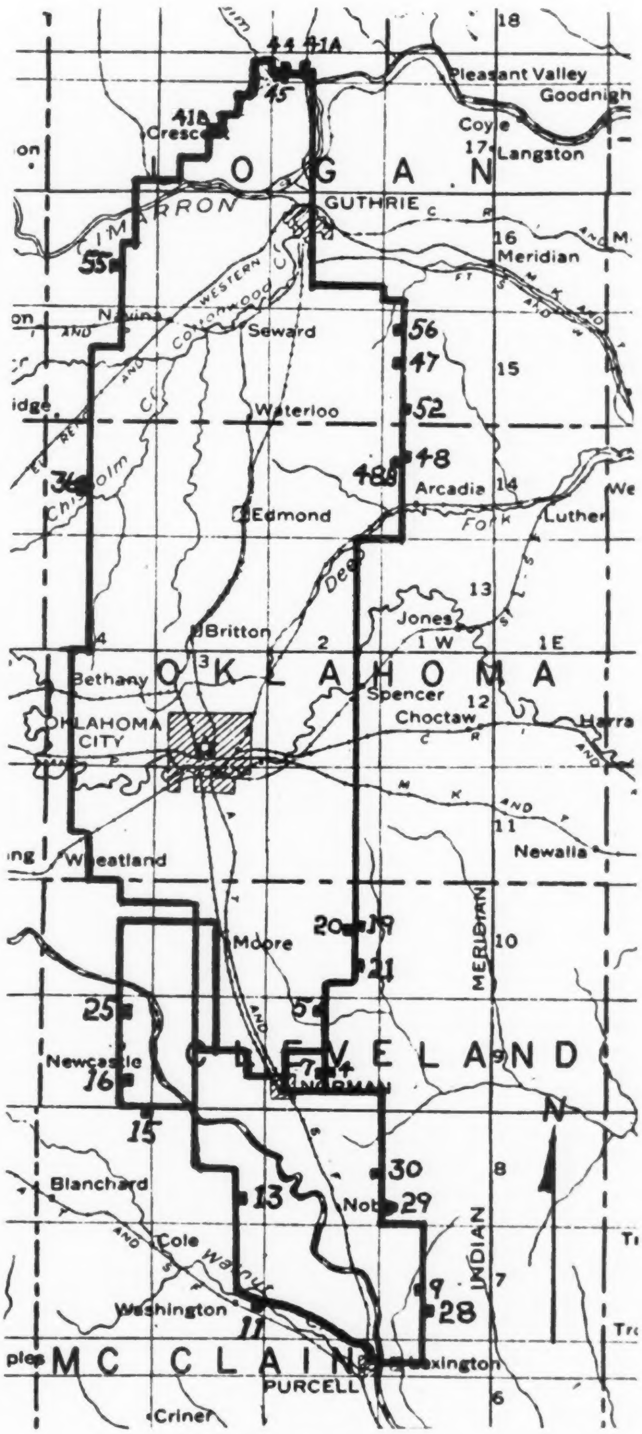

FIG. 1. Map showing the location of the areas studied in connection with the research reported in this paper.

light colored and sandy. In many places they are subject to severe erosion if not properly handled. These are mostly fine sandy loams. Erosion has caused and is causing much damage to farm lands in this region. The soils are not highly productive naturally but they produce fairly good yields of general farm crops until depleted by erosion or exhaustive cropping.

As is characteristic of the Cross-Timbers region in general, Windthorst and Nimrod soils are covered with a mixture of timber and grassland. A great deal of grassland has been converted into farmland. This land is more productive than timbered areas which were cleared and plowed. In either case the soil is easily eroded when deprived of its cover of vegetation and hence we find many abandoned areas which are slowly being reclaimed by native vegetation.

The original humus content of these soils was comparatively low and following erosion is so depleted that a comparatively long time must elapse before native vegetation can again occupy them. The open character of these soils promotes rapid oxidation of the organic matter, hence humus accumulation is slow.

The eastern portion of Cleveland, Oklahoma and Logan counties are occupied by the Hanceville-Conway group of soils. About one half of the stations used in this paper are located in this region which lies in the area known as the Cross Timbers and is a north-south belt of rolling, hilly or ridgy land for most part covered with scrub-oak timber. To the east lies a rather extensive tall-grass prairie and to the west so-called mixed-grass prairie. Of the soils the Yearbook of the United States Department of Agriculture states:

> Probably about one-third of the land is fairly smooth upland and has deep soils, about one-third shallow, stony, and gravelly soils, about one-sixth rough stony land and about one-eighth to one-sixth alluvial bottom lands. On smooth land the rocks have weathered deeply and the soils are largely fine sandy loams over mellow crumbly clay subsoils and moderately productive. The rough land is thin and largely non-arable.

The soils of this region are easily eroded and present as sad a picture of soil erosion as any in Oklahoma.

The portions of Logan and Oklahoma counties not occupied by Hanceville-Conway soils group and by soils modified by the presence of wide sandy rivers are occupied by Zaneis-Renfrow and associated soils. These soils have been developed from beds of red calcareous clay or sandy clay with occasional strata of gypsum, limestone or sandstone. These are known as the Red Beds formation. The soils are described by the Yearbook as being deep on smooth land, with red or brown surface soils, largely of silt loam or very fine sandy loam texture, over red and brown crumbly clay or sandy clay subsoils. Such land is fairly productive but is susceptible to erosion where rolling.

Although most of this region was originally occupied by little bluestem prairie, one does not receive the impression of continuity that one gets when

passing through prairies further west. There are innumerable small streams, dry most of the year, extending up valleys, which provide pathways for timber to extend out into the prairie. Thus as one travels over the prairies it seems as though they were bounded on all sides by strips of timber.

Prairie soils of this region have a rather high humus content (5 percent) and produce excellent yields of small grains. Corn culture is not so successful because of hot, dry winds and early summer droughts. Abandoned eroded land in this region still contains considerable humus and revegetation is much more rapid than in the case of Windthorst-Nimrod or Hanceville-Conway areas.

The higher water-holding capacity and less open character of soils of the western part of the study area are reflected in the character of the vegetation. Sandy soils take up and give up water easily. Such soils are occupied in most cases by oak woodland. Soils with a high clay content give up water to plants less readily and are occupied in this region by grasses.

The study areas or stations were selected in late winter and were chosen on the basis of appearance of soil and previous year's vegetation.

It would be desirable to limit the study to areas which were grassland before being plowed. In most cases this has been done but in other cases scrub oak may have covered the area prior to cultivation.

The woodland soil in this region is what might be termed poor since it lacks topsoil rich in humus such as characterizes prairie. Various workers have shown that humus content of agricultural lands tend to reach an equilibrium. The time required and the final content will depend upon climate, type of crop and initial content of humus. Unless precautions are taken to maintain humus content at the proper level, soils in central Oklahoma rapidly become impoverished. When this condition is reached agriculture is no longer possible. Such land is usually then abandoned. The humus content diminishes rapidly in soils of central Oklahoma when farmed because (1) comparatively high temperatures and moisture content do not permit rapid accumulation of organic matter, (2) the physical texture of the soil is favorable for erosion, hence much of the top soil with its humus is lost through erosion and (3) very little crop residue is returned to the soil each year. Since the humus reserve was low at the time the land was plowed, it does not take long to deplete it to such an extent that agriculture is no longer profitable.

Areas which have been abandoned for a time sufficient for the redevelopment of original prairie vegetation are non-existent in central Oklahoma. The three northern counties of the group studied, Logan, Oklahoma, and Cleveland, are a part of old Oklahoma Territory and were opened to settlement in 1889. Erosion was a problem present from the beginning of agricultural occupation in this region. Just how soon the first land was abandoned is not known.

At the beginning of the study, areas were selected to form a series from the most recently abandoned to the longest abandoned. The locations of all stations are shown in Figure 1.

The following brief description supplement data concerning stations and stages given elsewhere. The stage in succession to which each area belongs is indicated at the end of the description by a letter. *A* is the pioneer community and *F* the climax.

Area No.	
4	Eroded field, abandoned 2-3 years, slopes to the east, ½-1% grade. Stage A.
5	Prairie, check area. Stage F.
7	Prairie, check area. Stage F.
9	Eroded field, abandoned 10-12 years, 1-2% slope to the northeast. Stage D.
10	Eroded field, abandoned 8-10 years, sodded to Bermuda grass.
11	Eroded field, abandoned 10-12 years, 2-3% slope to the northeast. Stage B.
13	Eroded field, abandoned 8-10 years, 1-2% slope to the southeast. Stage B.
15	Prairie, check area. Stage F.
16	Eroded field, abandoned 15+ years, 1% slope to the east. Stage D.
19	Eroded field, abandoned 12+ years, terraced, 1-2% slope to the northeast. Stage D.
20	Eroded field, abandoned 8-10 years, 2-3% slope to the west. Stage C.
21	Old eroded field, abandoned 20+ years, Stage E.
24	Eroded field, abandoned 15+ years, 2-3% slope to west, terraced, pastured this year. Stage D.
25	Eroded field, abandoned 2-3 years, terraced, 1-2% slope to the east. Stage A.
26	Eroded, abandoned field. Stage D.
27	Prairie, check area. Stage F.
28	Prairie, check area. Stage F.
29	Prairie, check area. Stage F.
30	Old eroded field, abandoned 25+ years, some erosion between bunches of *Andropogon scoparius*, slopes 2-3% to south. Stage E.
36	Prairie, check area. Stage F.
41A	Recently abandoned eroded field, abandoned 2-4 years, slopes 1-2% to northeast. Stage A.
41B	Prairie, check area. Stage F.
44	Eroded field, abandoned 8 years, slopes 1-2% to the east, terraced. Stage C.
45	Prairie, check area. Stage F.
47	Old eroded field, abandoned 25+ years, 2-3% slope to south. Some erosion at present. Stage E.
48	Eroded field, abandoned 10-12 years, slopes 1-2% to north. Stage C.
48B	Eroded field, abandoned 8-10 years, slopes 2-3% to north. Stage B.
52	Old eroded field, abandoned 25-30 years, slopes 2-3% to southeast. Stage E.
55	Prairie, check area. Stage F.
56	Prairie, check area. Stage F.

METHODS

Beginning the 15th of March, 1938, the areas were studied at two-week intervals. At each visit, insect and plant collections were made. Notes on presence of animals, evidences of their activity, such as burrows, nests and droppings, and records of blooming dates and relative abundance of plants were made. Soil samples were collected in July. Most areas were trapped for small mammals in October. Pellet counts for the population of rabbits were made the last week in October. After the first of November the areas were revisited at thirty-day intervals.

Insect collections were made only in the herb layer, the ground species being neglected with exception of mound-building ants. Insect collections were made with an insect net 14 inches in diameter and having a handle 48 inches long. Fifty sweeps constituted a sample. Each sweep was approximately six feet in length and sweeps spaced at six foot intervals. Each collection was transferred to a cyanide killing jar and later wrapped in paper toweling, numbered and placed where air currents dried the material rapidly. After each field trip, the insect collections were sorted as soon as possible, trash removed, the number of each species recorded and the collection stored. Several specimens of each species were mounted.

The grasshoppers taken during this study received special study because Mr. Gerald Acker, a fellow worker, traveled with the writer throughout the course of the fieldwork and followed seasonal succession of these insects. His thesis, "Seasonal Succession of Grasshoppers in Central Oklahoma" is on file in the library of the University of Oklahoma.

Plants were collected at time of blooming from each area. They were placed in a press immediately after collecting and were dried as rapidly as possible. They were stored and later identified by the writer. About 3,000 specimens were collected. They have been placed in the Herbarium of the University of Oklahoma. Grasses of doubtful identity were checked by Mrs. Agnes Chase of the National Herbarium, Washington, D. C.

Soil samples were taken to a depth of six inches with a hollow cylinder sampler. A composite sample was made from each area by taking several samples and putting them all in one paper sack. Mechanical analyses by the hydrometer method as outlined by Bouyoucos (1936) were made. The loss on ignition was also determined.

The small mammals were trapped with mouse traps. Some rat traps were set without success, so their use was abandoned. Ordinarily twenty traps were set on each area for two successive nights. Oatmeal and raisins were used as bait. Peanut butter and nut meats were tried but were found to be less attractive to rodents than the oatmeal and raisin mixture.

Skins were made of all specimens taken in the traps. These skins have been placed in the Museum of Zoology, University of Oklahoma. The mouse skins were identified by H. H. T. Jackson of the Biological Survey, Washington, D. C.

Counts of fecal pellets were made by the method suggested by Taylor (1930). A wire frame having an area of 72 square inches was used to delimit areas on which they were counted. Twenty-five counts were made on each study area. Relative abundance of gophers, moles and ground squirrels was determined from their workings on each area.

Nests and presence of birds were also noted. Mr. Thomas Baskett traveled with the writer during the spring and early summer of 1938 and studied the meadowlarks throughout this region, including the study areas of the

writer. His thesis, "The Meadowlarks of Oklahoma," is on file in the library, University of Oklahoma.

The vegetation was analyzed rather carefully during the growing season and the relative abundance of each species was determined at the peak of its blooming period. This was done on each area without regard to the absolute density of each species. In September the total density of the vegetation and of the most important species were estimated for each area. Relative abundance was indicated by a scale of 5 for the most abundant species, usually the dominants, 4 for the subdominants, 3 for species common but not of dominant or subdominant rank, 2 for those occurring rather frequently throughout the community but seldom forming more than 1 percent of the vegetative cover, and 1 for plants contributing less than 1 percent of the vegetation.

The total coverage was indicated as percentage of area completely covered by the herbage when projected onto the ground. Correlated with the change from spring to summer and summer to fall aspects of vegetation is the change in insect populations. These changes will be taken up in the discussion of the various communities.

In presenting the data, the stations were first arranged according to degree of development toward the climax prairie community. It was found impractical to discuss data for each station separately, so the stations in the series were grouped arbitrarily into stages, A, the pioneer, to F, the climax prairie. Data for each stage were made up of totals for all stations included in that stage of succession. Since the number of stations per stage varied, data were all calculated on the basis of four stations per stage.

The following grouping of stations into stages was made. Figure 1 shows the location of these stations.

Stage A—4, 41A, 25.
Stage B—13, 48B, 11.
Stage C—44, 20, 48.
Stage D—19, 9, 24, 16.
Stage E—47, 30, 21, 52.
Stage F—29, 56, 5, 55, 36, 45, 7, 28, 41B.

Throughout this paper the term "Stages in Succession" is used frequently. These stages are arbitrary, that is, succession is a continuous process and its division into stages is for convenience in describing the changes occurring as communities develop. No seral community is permanent. Constant change is one of the features of all stages in succession. Changes occur much more rapidly in the earlier stages and become progressively slower as the climax is approached.

The subclimax community may under certain conditions be maintained for a long period of time. Fire and erosion are two important factors operating to maintain a subclimax condition by destroying soil organic matter

necessary for the establishment of climax prairie. A climax community maintains itself as long as climatic conditions remain the same and outside forces do not alter conditions within the community.

The dynamics of plant succession through the various stages may be expressed as follows:

A—Invasion of area by pioneer organisms.

B—Invasion of pioneer community by midseral species.

C—Domination of community by midseral species.

D—Invasion of midseral community by perennials characteristic of climax community.

E—Transition from community dominated by annuals to one dominated by perennials.

F—Climax grassland association.

NUMERICAL DATA

Succession of Animals

General

Groups of related organisms vary in their reactions to factors of the environment. This is true even of members of the same group. Every species differs from all others in its manner of responding to conditions in a habitat. A number of species may react to certain factors in the same way yet each may be affected differently by others. For such reasons, every species must be studied before conclusions can be drawn about any group of related organisms.

One of the obvious results of an environment unfavorable to a species will be a reduction in the rate of its reproduction. If the environment is unfavorable to a number of related species, there will be a decrease in the total number of individuals of that group to be found in the unfavorable habitat. On the other hand, the same conditions may be favorable to other species and as a result these species would show an increase. Mixed responses within a group of related species may be compensating to the extent that little difference in the total number of specimens may be found in different habitats.

Before taking up in detail the members of the various groups, the total number of specimens in each of the orders of arthropods are compared in each stage of succession.

Table 1 presents these data. The figures include in most groups the identified specimens. Exceptions to this are Hymenoptera, Lepidoptera, Arachnida and certain Diptera which are presented as total number of specimens taken.

TABLE 1. COMPARISON OF THE TOTAL NUMBER OF SPECIMENS IN EACH ORDER IN EACH STAGE IN SUCCESSION.

Succession stage	A	B	C	D	E	F
Coleoptera	304	274	308	452	384	758
Hemiptera	216	270	409	571	278	315
Homoptera	222	228	321	519	396	598
Hymenoptera	44	53	46	50	56	63
Diptera	145	157	228	193	151	220
Orthoptera	568	764	992	899	650	862
Lepidoptera	28	80	40	55	43	46
Arachnida	350	519	634	734	556	614
Totals	1,877	2,364	2,978	3,473	2,514	3,476

The Coleoptera and Homoptera tend to increase in abundance continuously from the initial stage in succession to the climax. Other orders in general show an increase in representatives from the initial stage to the midseral stages and then a decline toward the climax.

A drop in numbers which occurs in all groups in the subclimax stage E is puzzling until it is pointed out that in this stage the density of the vegetation declines as the perennial grasses replace the annual plants. The organic matter content of the soil and its waterholding capacity are still low in this stage, so perennial grasses, chiefly *Andropogon scoparius,* are rather widely spaced and have a bunch growth form. Roots of the grasses occupy the surface layer of the soil in a wide zone about each bunch of grass. Annual plants are not able to grow between the bunches of perennial grasses already occupying the soil. For this reason, interstitial plants which are present when the bunches of perennial grasses invade are very widely scattered or are absent. This accounts for the drop in total density of vegetation which in turn probably accounts for the drop in totals of the insect groups in this stage. As more organic matter accumulates in the soil, water-holding capacity increases and in the climax community roots of perennial grasses tend to occupy much deeper soil layers and the bunch growth form is lost as the bunches spread until most of the soil surface is occupied. The increase in density of vegetation is accompanied by an increase in insect numbers (Stage F).

The numbers of important species are shown for the abundant orders in each stage in succession in Table 2.

The column at the right side of the table shows total number of species of each order involved in succession. This gives some idea of how the total number of species in each stage compares with total for all stages.

The number of species of each order increases from the initial stage to midseral stages and then declines as a climax is approached. This change is shown even in subclimax stage E where it will be recalled the total number of specimens showed a drop in all orders, thus indicating that there is a

TABLE 2. NUMBER OF SPECIES OF EACH ORDER IN EACH STAGE OF SUCCESSION FROM ABANDONED ERODED LAND TO CLIMAX NATIVE PRAIRIE.

	A	B	C	D	E	F	Total
Coleoptera	45	49	49	75	63	45	118
Hemiptera	23	20	34	35	31	26	42
Homoptera	16	19	17	20	20	17	22
Hymenoptera	16	15	16	20	21	10	42
Diptera	24	20	21	26	25	26	39
Orthoptera	16	18	28	27	27	21	30
	140	141	165	203	187	145	293

decline in the number of specimens of each species present in stage E rather than a decrease in the number of species.

It must be remembered that all figures presented thus far represent only the more abundant species and that Lepidoptera and Arachnida are not divided into species and do not contribute to the figure for the total.

Since all species in the initial stage do not survive in the climax, it is necessary to show the number invading each stage in succession and how many survived in the climax. Table 3 presents these data by orders and the total for orders for all stages. Lepidoptera and Arachnida are omitted.

TABLE 3. TABLE SHOWING NUMBER OF SPECIES OF EACH ORDER INVADING EACH STAGE IN SUCCESSION.

	A	B	C	D	E	F
Coleoptera	45	20	17	17	13	6
Hemiptera	22	4	9	4	1	2
Homoptera	16	4	1	1	0	0
Hymenoptera	16	12	7	16	9	2
Diptera	24	4	3	4	1	1
Orthoptera	15	4	8	..	2	0
Totals	138	48	45	42	26	11

It is evident that the number of invaders decreases with each stage in succession as the climax is approached.

To show the number of invaders of each stage surviving in the climax, Table 4 has been prepared.

TABLE 4. THE NUMBER OF SPECIES INVADING EACH STAGE IN SUCCESSION, THE PERCENTAGE OF THE TOTAL INVOLVED, THE NUMBER AND THE PERCENTAGE OF THOSE INVADING WHICH SURVIVE IN THE CLIMAX.

Stage in succession	Number of species invading each stage	Percentage of total species	Number surviving in climax	Percentage survival
A	138	48.4	84	60.4
B	48	14.9	21	43.7
C	45	14.5	17	37.7
D	42	13.5	8	19.0
E	26	8.4	3	11.5
F	11	3.5	11	....

This table brings out the fact that fewer and fewer species invade each succeeding stage and that of those invading, a smaller percentage survive in the climax with each succeeding stage. It would seem that the later in succession a species invades the better should be its chances of survival. Apparently this is not true in all cases.

Coleoptera

The Coleoptera were found to be the most numerous group of insects as far as species are concerned, 118 or 40.3 percent of the 293 species treated belonging to this group. Of course, this percentage would be somewhat less were Lepidoptera sorted into species. The number of species of Coleoptera that invade each stage in succession are shown in Table 5.

TABLE 5. THE NUMBER OF SPECIES OF COLEOPTERA INVADING EACH STAGE IN SUCCESSION, THE PERCENT OF TOTAL COLEOPTERA CONCERNED, THE NUMBER AND THE PERCENT OF THOSE INVADING WHICH SURVIVE IN THE CLIMAX.

Stage of invasion	Number invading	Percent of total Coleoptera	Number surviving in climax	Percent of number invading
A (Pioneer)	45	38.	20	44.44
B	20	20.	10	50.00
C	17	14.4	3	18.00
D	17	14.4	4	23.40
E	13	11.	2	15.40
F (Climax)	6	5.08	6	100.00

The number of specimens of Coleoptera taken in each stage of succession shows an increase from pioneer stage to climax. There is a decrease in total number of specimens in subclimax stage E. The reason for this has been discussed in the general section dealing with data on insects.

Table 6 shows that there is an increase in number of species from pioneer stage (A) to the midseral stages, then a decrease in the climax. The number of specimens of Coleoptera shows an increase from pioneer to climax stage. Although the total number of families represented among the beetles collected is greater than presented in Table 6, the fourteen shown contain the majority of the specimens. Table 6 shows total number of families, species and specimens of Coleoptera considered in the data for each stage.

TABLE 6. THE NUMBER OF IMPORTANT FAMILIES AND SPECIES AND THE TOTAL NUMBER OF SPECIMENS OF COLEOPTERA COLLECTED IN EACH STAGE IN SUCCESSION.

Stages in Succession	A	B	C	D	E	F	Total
Number of families	12	11	13	14	13	12	14
Number of species	46	46	50	76	57	45	118
Number of specimens	304	274	308	452	384	758	2,480

The families of Coleoptera considered in succession from the pioneer stages on eroded, abandoned farmland include those shown in Table 7. The numbers of species and specimens of each family in each stage are also shown.

TABLE 7. THE NUMBER OF SPECIES AND SPECIMENS IN EACH FAMILY OF COLEOPTERA IN EACH STAGE IN SUCCESSION.

Family		A	B	C	D	E	F
Alticidae	species	5	7	6	7	6	7
	specimens	22	55	85	119	23	184
Buprestidae	species	1	..	2	2	2	1
	specimens	1	..	3	4	10	1
Carabidae	species	1	1	1	2	2	2
	specimens	1	1	1	5	18	4
Cerambycidae	species	1	..	3	3	3	3
	specimens	8	..	8	17	12	15
Chrysomelidae	species	16	16	15	27	19	13
	specimens	122	99	90	107	132	378
Coccinellidae	species	2	2	3	5	2	2
	specimens	4	10	9	11	9	5
Curculionidae	species	11	11	9	12	12	10
	specimens	47	30	31	58	97	99
Elateridae	species	2	..	..	2	1	..
	specimens	2	..	..	2	1	..
Melyridae	species	1	1	1	1	1	1
	specimens	32	32	30	58	24	28
Meloidae	species	2	2	4	8	3	3
	specimens	3	8	6	21	9	13
Mordellidae	species	1	1	1	1	1	1
	specimens	44	11	12	18	20	20
Mylabridae	species	..	1	1	1	..	1
	specimens	..	5	5	3	..	3
Phalacridae	species	3	3	3	3	3	1
	specimens	18	21	27	26	31	8
Scarabaeidae	species	..	1	1	2	2	..
	specimens	..	1	1	2	2	..
Total species per stage		46	46	50	76	57	45
Total specimens per stage		304	274	308	452	384	758

As may be seen from Tables 7 and 8, the most numerous group of Coleoptera in this study was the Chrysomelidae, one third of all species of beetles in each stage belonging to this group. In Table 8 are shown the species and the number of specimens of each collected in each stage.

Hemiptera

The phytophagous Hemiptera, because of the morphology of their mouthparts and their manner of use, inflict less visible wounds to the plants on which they feed than phytophagous Coleoptera and Orthoptera yet withdrawal of juices is probably as damaging as outright devouring of a portion of the plant. Hemiptera are also of interest because of the large number of predaceous species in the order.

A total of 42 species of true bugs occurred in sufficient numbers to be listed in this study. This is 15 percent of the total number of arthropods included, excluding Lepidoptera and Arachnida. The number of species of Hemiptera invading each stage are shown in Table 9, as well as the number and percent surviving in the climax prairie.

TABLE 8. NUMERICAL DISTRIBUTION OF THE SPECIES OF COLEOPTERA IN THE STAGES OF SUCCESSION

Family	Genus	Species	Stage In Succession						Months Collected (inclusive)
			A	B	C	D	E	F	
Chrysomelidae	Babia	quadriguttata	..	..	..	5	1	2	May, June
	Blepharida	rhois	1	1	1	1	..	..	June, July
	Cassidea	bivittata	..	1	..	1	..	..	June
	Chrysomela	auripennis	..	..	4	..	..	..	June, July
	Coptocycla	bicolor	..	..	..	..	2	..	June, July
	Diabrotica	12-punctata	1	4	1	7	3	8	May – July
	Diabrotica	vittata	..	..	3	..	..	6	June, July
	Diabrotica	atripennis	2	..	..	..	..	40	June, July
	Galerucella	notulata	4	20	3	4	3	..	May – September
	Graphops	varians	5	6	8	11	5	6	May – June
	Lema	immaculicollis	1	..	..	1	..	5	April, May
	Leptinotarsa	decimlineata	52	8	..	9	1	..	June, July
	Luperodes	varicornis	..	1	..	1	4	20	June – August
	Nodonota	clypealis	..	..	..	..	..	36	May – July
	Pachybrachys	morosus	15	17	29	9	38	56	May – August
	Cryptocephalus	venustus	..	..	..	..	4	1	July
	Pachybrachys	spp.	..	..	..	41	11	4	May – July
	Pachybrachys	autolycus	10	9	2	2	46	150	May – July
	Saxinis	omogera	1	..	3	2	2	..	May – August
	Typhophorus	canellus	..	..	..	1	2	32	May – September
	Zygogramma	disrupta	11	16	12	12	5	..	April – October
	Zygogramma	exclamationis	5	..	..	2	..	..	August – September
Alticidae	Phyllotreta	lewisii	9	5	21	13	12	4	May, June
	Chaetocnema	deticulata	5	12	16	37	2	8	May – July
	Altica	foliacea	8	3	2	6	3	56	April – July
	Oedionychis	gibbitarsa	..	5	..	8	..	1	May, June
	Oedionychis	sp.	..	3	1	4	1	2	July
	Pleurostichus	convexicaulis	2	5	48	27	5	32	May – September
	Systena	hudsonias	3	24	..	27	1	88	May – June
Carabidae	Discoderus	parallelus	..	1	..	2	9	..	May
	Lebia	viridis	..	..	..	..	1	4	June
Cleridae	Hydnocera	pubescens	..	1	..	1	1	..	May
Cerambycidae	Tetraopes	collaris	..	..	1	1	..	..	June
	Typocerus	sinuatus	..	..	6	14	9	8	June, July
	Saperda	populnea	8	..	1	2	..	2	June, July
Coccinellidae	Hyperaspis	undulata	..	..	5	4	2	..	August, September
	Hippodamia	convergens	3	7	21	4	7	4	June – August
	Olla	abdominalis	..	3	..	1	..	..	August
Curculionidae	Anthonomus	nigrinus	16	..	5	3	5	10	June, July
	Cetrinus	modestus	1	3	1	6	3	1	June – September
	Chalcoderma	aeneus	1	..	1	4	..	..	September
	Hormops	aducens	..	1	1	1	..	6	May, June
	Taniimecus	lacaena	..	2	5	18	11	16	May – September
	Mytostylus	tenuis	15	11	2	22	30	36	May – September
Buprestidae	Acmaeodera	pulchella	..	..	1	3	..	..	June, July
	Acmaeodera	neglecta	..	..	..	..	1	1	July
	Agrilus	politus	1	..	2	1	9	..	May – August
Mylabridae	Mylabris	obtectus	..	5	5	3	..	3	
Melyridae	Collops	quadrimaculatus	32	32	30	58	24	28	May – October

TABLE 8 *(Continued)*

Family	Genus	Species	Stage In Succession						Months Collected (inclusive)
			A	B	C	D	E	F	
	Epicauta	maculata	2	4	3	8	6	8	May – August
	Epicauta	trichrus	..	..	..	1	2	..	June, July
Meloidae	Epicauta	ferruginea	..	4	1	3	..	4	June – September
	Epicauta	funebris	..	..	..	1	1	..	July
	Macrobasis	immaculata	1	..	..	5	..	..	June
Mordellidae	Mordella	melaena	44	11	12	18	20	20	May – October
	Phalacrus	simplex	16	5	11	17	20	8	April – October
	Phalacrus	politus	2	23	16	9	11	..	July – September
	Phalacrus	sp.	5	4	12	4	7	..	July – September

TABLE 9. SHOWING NUMBER OF SPECIES OF HEMIPTERA INVADING EACH STAGE IN SUCCESSION, THE PERCENT OF TOTAL CONCERNED, AND THE NUMBER AND PERCENT SURVIVING IN CLIMAX.

Stage of invasion	Number invading	Percent of total hemiptera	Number surviving in climax	Percent of number invading
A (Pioneer)	23	52.3	18	80.0
B	4	9.5	1	25.0
C	9	21.4	2	22.2
D	4	9.5	0	25.0
E	1	2.4	0	0.0
F (Climax)	2	4.8	2	100.0

The number of specimens of Hemiptera per stage increases from pioneer to the midseral stages, then shows a decline toward the climax. The number of species in each stage shows a similar behavior. Table 10 shows these data.

TABLE 10. THE NUMBER OF FAMILIES, SPECIES, AND SPECIMENS OF HEMIPTERA IN EACH STAGE IN SUCCESSION.

	A	B	C	D	E	F	Total
Number of families	10	7	13	12	12	10	14
Number of species	23	20	34	35	31	26	42
Number of specimens	216	270	409	571	278	315	2,059

Of the twelve families of Hemiptera represented in the succession from abandoned eroded farmland to climax prairie, the Pentatomidae, Lygaeidae and Miridae are by far the most numerous in species and specimens. Almost all members of these three families are plant feeders and oftentimes are very damaging to certain crops. Many species of Hemiptera feed on a wide range of plants while others often are associated with one group. Table 11 shows the number of species and specimens of each family in each stage in succession.

TABLE 11. THE NUMBER OF SPECIES AND SPECIMENS IN EACH FAMILY OF HEMIPTERA IN EACH STAGE OF SUCCESSION.

Family		A	B	C	D	E	F
Lygaeidae	species	5	4	9	9	9	6
	specimens	27	74	62	96	29	92
Miridae	species	4	4	5	7	4	5
	specimens	24	32	49	103	46	65
Pentatomidae	species	7	6	8	9	8	7
	specimens	83	67	134	159	121	46
Reduviidae	species	1	2	3	1	1	1
	specimens	8	13	5	5	2	6
Cormelaenidae	species	2	2	2	2	2	2
	specimens	14	52	70	120	27	76
Tingididae	species	1	..	1	2	2	1
	specimens	1	..	1	9	5	2
Coreidae	species	1	1	1	1	1	1
	specimens	11	6	13	3	11	2
Corezidae	species	1	1	1	1	1	1
	specimens	29	26	44	53	29	20
Scutelleridae	species	1	..	1	1	1	1
	specimens	9	..	20	19	4	4
Nabidae	species	..	..	1	..	1	1
	specimens	1	..	3	..	3	2
Coriscidae	species	..	..	1	1	1	..
	specimens	..	..	1	1	1	..
Phymatidae	species	..	..	1	1	..	..
	specimens	..	..	7	3	..	..
Total species		24	20	34	35	31	26
Total specimens		216	270	409	571	278	315

Table 12 shows the number of specimens of each species in each stage in succession.

Orthoptera

The most numerous insects in all stages of succession from abandoned eroded farmland to climax prairie were the Orthoptera; 4,365 specimens or 30 percent of all studied belonging to this group. Five families and thirty species are represented. The Acrididae was by far the most numerous family, both in species and specimens. Many Orthoptera exhibit definite successional trends, certain species being restricted to definite communities.

The majority of Orthoptera are phytophagous while some, such as the Mantidae, are wholly predaceous. Many of the phytophagous forms will at times eat animal matter, this being especially true of the Gryllidae. The nymphs of Oecanthus feed on aphids according to Vestal (1913).

A large percentage of the Orthoptera were taken as nymphs, most of which are difficult to identify beyond family. In each family these have been included with the adults. No attempt was made to assign the nymphs to species in the Acrididae. If adults of all species were captured with the same ease as nymphs, we might expect the total number of nymphs to be composed of the same proportion of the various species as the adults. This,

TABLE 12. NUMERICAL DISTRIBUTION OF THE MORE IMPORTANT SPECIES OF HEMIPTERA IN THE STAGES OF SUCCESSION

Family	Genus	Species	Stage In Succession A	B	C	D	E	F	Months Collected	Months Most Abundant
Miridae	Adelphocoris	rapidus	8	1	...	5	4	25	May – November	August
	Lygus	pratensis	9	3	20	56	12	6	May – November	May
	Mimoceps	sp.	...	...	4	14	16	4	June – August	
	Poecilocapsus	lineatus	3	1	2	...	...	...	May, June	
	Polymerus	basalis	6	25	24	28	14	28	May – November	June-October
Pentatomidae	Mecidia	longula	26	16	24	40	37	24	July – November	August-Sept.
	Peribalus	abbreviatus	12	13	13	21	16	4	April – October	October
	Peribalus	limbolarius	...	...	16	7	4	...	May – September	July
	Prionosoma	podoploides	...	13	36	45	33	2	May – August	July
	Solubea	pugnax	...	...	...	2	2	...	July, August	
	Thyanta	custator	11	14	17	14	19	2	May – October	August
	Thyanta	sp.	16	...	11	4	...	...	July – October	July
	Trichopepla	semivitatta	13	6	13	25	5	12	June – October	June, July
Lygaeidae	Blissus	leucopterus	3	5	3	4	...	...	April – October	May, June
	Lygaeus	reclivatus	...	...	...	3	...	8	June, July	
	Ortholomus	scolopax	5	6	5	35	6	1	April – October	May, August
	Ortholomus	jamaicensis	13	12	20	23	5	72	June – October	Same all months
	Ortholomus	sp. No. 7	1	...	1	18	2	8	May – September	June
	Presma	cinera	...	...	15	4	6	2	May	May
Phymatidae	Phymata	erosa	...	...	7	3	6	...	July, August	August
Corimelaenidae	Corimelaena	quadrisignata	2	6	2	20	3	16	April – September	April
	Galgupha	nitiduloides	12	46	68	100	24	60	April – September	May, August
Nabidae	Nabis	ferus	1	...	3	...	...	2	May, June	
	Mygodenia	serripes	...	...	...	...	3	...	Sept. – November	
Tingididae	Gargaphia	solanii	1	...	...	7	4	2	May, June	
Reduviidae	Sinea	sp.	8	8	3	5	2	6	May – October	
Coreidae	Chariesterus	antennator	11	6	13	3	11	2	May – November	May, August
Corizidae	Harmostes	reflexulus	29	26	44	53	29	10	April – November	June, September
Scutelleridae	Homaemus	bijugis	9	...	20	19	4	4	May – October	May

of course, is not true since adults vary greatly in their ability to elude the net.

Table 13 shows the number of species and specimens in each family and total number of Orthoptera per stage in succession.

The number of species that invade each stage and the number that survive in the climax are shown in Table 14.

Table 14 gives evidence to show that the majority of the Orthoptera are tolerant of a wide range of soil conditions and can feed on many species of plants. Two thirds of the species taken in the pioneer stage were taken in all stages of succession including the climax. 90.3 percent of the species of Orthoptera invade pioneer and early midseral stages and of the total number of species taken in the climax, 95 percent are species that invaded early in

TABLE 13. THE NUMBER OF SPECIES AND SPECIMENS IN EACH FAMILY OF ORTHOPTERA IN EACH STAGE OF SUCCESSION.

Family		A	B	C	D	E	F	Total
Acrididae	species	14	16	22	22	21	15	24
	specimens	327	564	814	470	470	579	3,583
Gryllidae	species	1	1	1	1	1	1	1
	specimens	224	200	128	100	100	100	852
Mantidae	species	..	..	1	1	1	1	1
	specimens	..	..	2	3	2	2	9
Phasmidae	species	..	..	1	1	1	1	1
	specimens	..	..	10	17	38	90	156
Tettigoniidae	species	1	1	3	2	3	3	3
	specimens	1	1	10	17	13	70	112
Total species		16	18	28	27	27	21	30
Total specimens		568	764	992	899	650	862	4,635

TABLE 14. THE NUMBER OF SPECIES OF ORTHOPTERA THAT INVADE EACH STAGE IN SUCCESSION AND THE NUMBER THAT SURVIVE IN THE CLIMAX.

Stage invading	Number invading	Percent of total	Number surviving in climax	Percent of number invading
A	15	53.0	10	66.6
B	4	13.3	2	50.0
C	8	26.6	7	88.0
D	0	0.0	0	0.0
E	2	6.6	2	100.0
F	0	0.0	0	0.0

succession. No species of Orthoptera were exclusive to climax prairie. These data are presented in Table 15.

Diptera

Flies were very numerous in March, April and May but almost absent during the remainder of the year. The specimens considered in this study represent 40 species and 9 families. A few other species and families were represented by one or two specimens each but were not numerous enough to be considered. Table 16 shows the families, species, and spcimens of Diptera each in each stage of succession.

Among the species are found many which are predaceous either as adults or larvae. Larvae of others are very damaging to parts of plants. Details of the relationships of these forms to the biotic community are taken up later.

Homoptera

Species of Homoptera seem to be more adaptable to environmental factors than are those of other orders of insects. Of the twenty-two species involved in succession from abandoned eroded farmland to climax prairie, at least 70 percent occur in every stage from pioneer to climax. The number of specimens per stage shows an increase from pioneer to climax. A drop

TABLE 15. NUMERICAL DISTRIBUTION OF THE SPECIES OF ORTHOPTERA IN THE STAGES OF SUCCESSION

Family	Genus	Species	Stage In Succession						Months Collected (inclusive)
			A	B	C	D	E	F	
	Acrolophitus	hirtipes	..	4	2	5	13	12	April, May, August
	Ageneotettix	deorum deorum	3	3	10	4	4	3	June – August
	Arphia	xanthoptera	..	..	2	1	4	14	May – August
	Boopedon	gracile	..	..	1	1	..	2	June, July
	Chorotophaga	viridifasciata	..	1	60	21	4	2	March – August
	Hadrotettix	trifasciatus	6	3	7	2	1	..	July – September
	Hesperotettix	speciosus	13	15	7	13	7	2	June – August
	Hesperotettix	viridis pratensis	..	..	3	6	4	4	June, July
	Hesperotettix	viridis viridis	1	..	9	12	7	7	June – August
Acrididae	Melanoplus	angustipennis	1	..	13	13	10	..	July – October
	Melanoplus	bivitattus	7	8	4	14	3	10	May – October
	Melanoplus	confusus	20	18	57	44	41	75	March – June
	Melanoplus	differentialis	42	5	8	4	..	..	July – October
	Melanoplus	packardii	11	17	18	11	12	14	June – October
	Melanoplus	foedus fluvitalis	1	..	9	12	7	7	June – August
	Orphulella	speciosa	..	..	3	17	..	8	August
	Mermeria	maculipennis	4	18	34	80	18	26	June – October
	Pardalophora	saussurei	3	5	16	10	9	9	May – August
	Hippiscus	rugosus	..	2	9	25	2	..	July – October
	Schistocerca	americana	5	2	34	10	7	8	April – September
	Schistocerca	lineata	..	1	20	4	8	..	July – September
	Syrbula	admirabilis	3	14	8	36	10	46	June – October
Gryllidae	Oecanthus	nigricornis argentinus	224	200	128	100	100	100	May – October
Mantidae	Stagmomantis	caroliniana	..	..	2	3	2	2	July, August
Phasmatidae	Diapheromera	veili veili	..	..	4	4	38	90	March – June
Tettigonidae	Scudderia	texensis	..	..	2	9	5	46	April – July
	Conocephalus	strictus	..	..	7	8	5	18	May – July
	Neoconocephalus	robustus crepitans	..	..	1	..	3	6	July

TABLE 16. THE NUMBER OF SPECIES AND SPECIMENS IN EACH FAMILY OF DIPTERA IN EACH STAGE IN SUCCESSION.

Family		A	B	C	D	E	F	Total
Asilidae	species	1	1	1	2	2	3	3
	specimens	5	1	1	3	5	8	23
Sarcophagidae	species	11	8	8	12	9	9	14
	specimens	41	49	103	72	29	54	348
Otitidae	species	2	0	1	0	1	1	2
	specimens	41	0	3	0	2	2	[illegible]
Muscidae	species	3	5	5	5	6	5	7
	specimens	29	67	43	30	31	51	251
Tabanidae	species	2	0	1	3	3	2	8
	specimens	4	0	1	3	8	3	20
Syrphidae	species	1	2	2	2	2	2	2
	specimens	8	2	14	15	9	10	88
Trypaneidae	species	2	2	2	1	1	2	2
	specimens	4	25	16	19	11	21	96
Bombyliidae	species	1	1	1	..	..	1	1
	specimens	3	1	3	..	..	6	13
Helomyzidae	species	1	1	1	1	1	1	1
	specimens	10	12	44	51	68	64	249

TABLE 17. MONTHS IN WHICH REPRESENTATIVES OF THE PRINCIPAL FAMILIES OF DIPTERA WERE TAKEN.

Ascilidae	April, May, June, July
Sarcophogidae	April, May, June, July, August
Otitidae	April, May, June, July
Muscidae	April, May, June, July, August, September
Tabanidae	July, August
Syrphidae	May, June, July, August, September
Trypaneidae	May, June, July, August, September
Bombyliidae	August, September
Helomyzidae	May, June, July

in the total number of Homoptera in subclimax stage E occurs as it does in other insect orders.

Five families are represented among the twenty-two species of Homoptera considered. It might be mentioned at this point that for some reason the number of Homoptera was unusually low this year (1938). This was also true of the Diptera. Perhaps the large proportion of spiders accounts for the decrease in these groups. The unusually moist spring and summer probably promoted attacks of fungi.

The Cicadellidae was by far the most numerous group of Homoptera both as to total species, 68 percent of the species belonging to the Cicadellidae and to specimens, approximately 50 percent of the total specimens of Homoptera belonging to these species. Table 18 summarizes the data on families, species and specimens in each stage of succession.

TABLE 18. THE NUMBER OF FAMILIES, SPECIES AND SPECIMENS OF HOMOPTERA IN EACH STAGE.

Stage	A	B	C	D	E	F	Total
Families	4	5	5	5	5	5	5
Species	16	19	17	20	20	17	22
Specimens	222	228	321	519	396	598	2,284

The number of species and specimens in each family in each stage are shown in Table 19.

TABLE 19. NUMBER OF SPECIES AND SPECIMENS IN EACH FAMILY OF HOMOPTERANS IN EACH STAGE IN SUCCESSION.

Family		A	B	C	D	E	F
Cicadellidae	species	10	12	10	13	13	10
	specimens	160	122	200	291	142	278
Membracidae	species	3	3	3	3	3	3
	specimens	53	82	49	212	106	98
Fulgoridae	species	3	3	2	3	3	2
	specimens	10	15	13	13	42	6
Cercopidae	species	0	1	1	1	1	1
	specimens	0	9	50	3	120	200
Aphididae	species	1	1	1	1	1	1
	specimens	*	*	9*	*	*	16*

* Not counted.

Table 20 shows the number of each species in each stage in succession.

TABLE 20. NUMERICAL DISTRIBUTION OF THE SPECIES OF HOMOPTERA IN THE STAGES OF SUCCESSION ON ABANDONED ERODED FARMLAND

Family	Genus	Species	Stage In Succession						Months Collected (inclusive)	Months Most Abundant
			A	B	C	D	E	F		
Cicadellidae	Chlorotettix	unicolor	18	22	32	68	46	139	June – November	June, August
	Deltocephalus	inimicus	15	36	96	117	24	30	May – October	June, August
	Deltocephalus	sp. No. 14	...	1	26	8	12	...	May, June	May
	Deltocephalus	sp. No. 15	11	...	5	9	3	4	May – October	May, September
	Driotura	robusta	30	7	...	7	...	...	July – October	August, Sept.
	Empoasca	viridescens	40	4	16	11	4	36	April – November	April, May
	Euscelis	obscurinervis	9	6	1	25	6	12	April – November	April, May
	Helochara	communis	...	7	...	10	4	...	May – September	July, August
	Helochara	sp.	3	2	3	1	1	...	June – October	July
	Mesamia	nigridorsum	20	17	16	17	18	12	May – October	May
	Oncometopia	lateralis	8	4	...	...	4	10	April – November	
	Thamnotettix	inornatus	...	...	...	1	10	16	May	
	Xerophloea	major	...	3	3	7	1	18	May – July	June
	Xerophloea	viridis	6	13	2	10	10	2	April – November	June, November
Membracidae	Campylenchia	latipes	16	57	9	162	60	54	June – November	August, Sept.
	Stictocephala	festina	8	13	12	45	34	40	April – November	September
	Vanduzea	arcuata	29	12	28	5	12	4	May – November	September
Fulgoridae	Scolops	spurcus	2	12	9	8	22	4	June – November	July, September
	Scolops	sp.	7	2	...	3	1	...	July – October	September
Cercopidae	Aphrophora	quadrinotata	...	9	50	3	120	200	May – October	July

Hymenoptera

The specimens of Hymenoptera are few in number as compared to other insects considered in this study. The role played by these insects in a biotic community is indeed a complex one. Some species are predators, other parasitic. Some feed only on plant material. A great many species deposit their eggs in some portion of a living plant, at the same time stimulating the plant tissue to produce a characteristic enlargement we call a gall. This houses and feeds the developing larva. Insects from tiny aphids to the largest grasshoppers are parasitized by Hymenoptera. The cuckoo wasps utilize the food and nests of other Hymenopterans.

Since ants are largely ground dwellers, not enough specimens were taken to be considered. However, collections were made of the large mound-building ants. These were found to be more abundant in early stages of succession. They prefer open ground for their nests and keep the soil clear of vegetation for some distance around the mound.

Anyone who has attempted to classify a Hymenopteran will understand the difficulty in obtaining names for many species when most of them are represented by only one or two specimens. The families listed in Table 21 are discussed in another section of the paper. A total of 43 species are represented among the Hymenoptera considered.

TABLE 21. THE NUMBER OF SPECIES AND SPECIMENS IN EACH FAMILY OF HYMENOPTERA IN EACH STAGE OF SUCCESSION.

Family		A	B	C	D	E	F	Total
Psammocharidae	species	2	..	..	1	1	1	2
	specimens	2	..	..	6	1	1	10
Braconidae	species	1	3	3	4	3	2	8
	specimens	4	3	8	5	8	2	30
Ichneumonidae	species	3	2	2	4	2	3	6
	specimens	9	5	4	7	7	12	40
Tenthredinidae	species	..	1	1	..	2	..	4
	specimens	..	1	4	..	5	..	10
Chalcididae	species	3	4	3	3	3	2	6
	specimens	15	5	4	5	4	8	41
Dryinidae	species	..	..	1	2	..	..	2
	specimens	..	..	1	5	..	..	6
Andrenidae	species	2	2	3	3	4	2	5
	specimens	11	36	21	22	23	39	152
Chrysididae	species	1	..	1	..	1	..	1
	specimens	1	..	1	..	1	..	3
Scoliidae	species	2	2	2	1	2	1	4
	specimens	3	5	4	4	5	2	23
Mutillidae	species	..	..	1	2	1	..	3
	specimens	..	..	3	5	1	..	9
Myrmicidae	species	2	1	1	1	1	..	2
Total specimens		45	55	50	59	55	64	328
Total species		16	15	16	21	20	11	43

Lepidoptera

Lepidoptera were in no stage in succession found to be numerous. Adult specimens were usually too mutilated to be identified when taken in routine sweeping. For these reasons, no attempt was made to identify them.

Lepidoptera exert their greatest influence on vegetation during their larval life. The ravages of such forms as army worms, cut worms, etc., are well known. Lepidopteran larvae furnish food for many predaceous forms. Many of these larvae are parasitized by various Hymenoptera and Diptera, such victims dying lingering deaths.

There was found to be some difference in the number of Lepidoptera from one stage in succession to another. The difference in species is not known. It is a well-known fact that many select specific food plants.

The number of Lepidoptera was rather low throughout the region covered by this study. Table 22 shows the number of specimens taken in each stage in succession.

TABLE 22. NUMBER OF SPECIMENS OF LEPIDOPTERA IN EACH STAGE.

Stage	A	B	C	D	E	F
Number of specimens	28	80	40	53	43	46

The number of Lepidoptera captured at any one collection was found to be influenced considerably by the number of plants in bloom, especially those offering nectar as an attraction to insect visitors. Stages in succession

offering plants in bloom over a long period of time show the greatest total number of lepidopterous specimens.

Arachnida

Spiders are of interest because of their predaceous habits. Their dependence upon insects for food means that their numbers will be governed to an extent by the number of insects available. In turn those forms preyed upon will have their abundance reduced. This is one of the systems of checks and balances found in nature. Spiders are used extensively by Hymenoptera as food for their larvae. These same wasps are parasitized by other hymenopterans and species of Diptera.

Table 23 shows the total number of insects and of spiders taken in each stage in succession.

TABLE 23. TOTAL NUMBER OF INSECTS AND SPIDERS IN EACH STAGE.

Stage	A	B	C	D	E	F
Total insects	1527	1845	2344	2739	1958	2862
Total spiders	350	519	634	734	556	614
Ratio	7/30	7/26	7/26	7/26	7/25	7/32

Table 23 shows that the number of spiders is directly proportional to the number of insects present. The correlation between seasonal distribution of spiders and the peaks in insects numbers has not been calculated.

Amphibia

The nocturnal habits and peculiar habitat conditions necessary for their breeding made obtaining an accurate census of Amphibia impossible. Areas suited to the feeding activities of adults of various toads in most cases had no depressions or ponds in which they might breed. In the mixed grass prairie, which is the prairie climax in central Oklahoma, *Bufo cognatus* is abundant and can be taken from roadways after spring and summer rains. *Bufo woodhousii* is also common throughout this region, not only in the prairie but also in woodland. *Scaphiopus bombifrons Microhyla olivacea* and *Acris crepitans* were found in great abundance around buffalo wallows and along roadside ditches in prairie regions following heavy rains in spring and summer. These species are almost never seen during dry weather or during daytime.

In the study areas, terrace ditches were present in some cases and served as breeding grounds for amphibians. Tadpoles of *Scaphiopus bombifrons* were found in a terrace ditch on May 15, 1938 in area 44. The young were not seen after they metamorphosed. *Bufo woodhousii* bred in a pool behind a terrace in area 16. Both of these areas are in midseral stages of succession.

Amphibia feed largely on insects and for this reason are of considerable importance in a biotic community. As was mentioned elsewhere, *Bufo cognatus* and *B. woodhousii* were both observed to feed on large mound-building

ants (*Pogonomyrmex* spp.). It was not possible to obtain data to show successional behavior of any species of Amphibia.

Birds

The only species of bird occurring in any abundance in any of the stages of succession of abandoned eroded farmland to climax prairie was the eastern meadowlark, *Sturnella magna magna.* Nests of three mourning or turtle doves and one dickcissel were found.

Almost without exception, meadowlarks nested in midseral stage areas, those characterized by an abundance of Aristida and Eragrostis. These stages had a small population of rodents until fall, at which time cotton rats *(Sigmodon hispidus texianus)* invaded from nearby areas. Normally these stages would have a small population of rats.

The mourning or turtle dove *(Zenaidura macroura marginella)* is apparently not specific in its nesting sites. Nests were found in pioneer, midseral and climax stages. These birds often nest in stubblefields where small grains have been harvested. They usually build no nest when nesting on the ground, the eggs being placed directly on the ground, sometimes under the shade of a plant, oftentimes not. The adults feed on seed of various kinds.

Table 24 shows the number of nests of each species in each stage in succession.

TABLE 24. NUMBER OF NESTS OF BIRDS IN THE STAGES OF SUCCESSION.

Species Stage	A	B	C	D	E	F
Eastern meadowlark			3	5	*	*
Mourning dove	1			1	1	
Dickcissel						1

* Nests present but not located and counted.

Many times marsh hawks *(Buteo hudsonicus)* were observed hunting over prairies. The only animals which they were observed to catch were rodents, probably cotton rats as these are active during the daytime. Hawks were disturbed at different times while feeding on (1) a toad *(Bufo woodhousii)*, (2) a snake and (3) rabbits. Sparrow hawks (*Falco sparverius* L.) and occasionally sharp shinned hawks *(Accipter velox)* were seen hunting over the study areas during the summer and fall. Meadowlarks as well as quail frequently fall prey to these hawks.

A good many vesper sparrows were noted in the grassland but no nests were found, although one female was taken while sweeping for insects (Stage D).

The desert horned lark *(Otocoris alpestris leucolaema)* is a summer resident of the prairies of central and western Oklahoma (Nice 1931). No nesting larks were found although adults were not uncommon along prairie areas.

Reptiles

Not many data on reptiles were obtained during this study. Their relatively small number and retiring nature prohibit obtaining any accurate count.

All specimens of snakes encountered were captured and placed in the Museum of Zoology, University of Oklahoma. Lizards which could be captured were brought in to the laboratory. Unfortunately, very few specimens of reptiles were taken from study areas.

The striped green lizard, *Cnemidophorus sexlineatus sexlineatus* L. was common and was apparently most abundant in stages in succession in which a considerable portion of soil surface was exposed. Two specimens of *Holbrookia maculata* were taken in very much overgrazed pastures. Many specimens of *Crotaphytus collaris collaris* (Say) were found around rocky outcrops, but they are not a portion of the prairie community but are characteristic animals of rocky areas.

The box turtle, *Terrapena ornata* Agassiz, was found in all types of habitats, seeming to show no preference.

Pituophis sayi sayi (Schegel), the bull snake, is rather common on prairies and plains. Only one specimen was taken from areas concerned in this study. A rabbit was heard crying in tall prairie grass. Upon investigation, a half-grown rabbit was found in the coils of a large bull snake. It was released when the snake was picked up. The rabbit appeared to be much too large for the snake to swallow but where snakes' mouths are concerned, looks are deceiving. Another large bull snake was taken from a roadway. This snake showed a number of bulges in its midsection. Dissection revealed six young rabbits, each a little larger than a rat.

Although not numerous, reptiles play an important part in a biotic community. Lizards feed principally on insects. They fall prey to other larger animals, such as birds, snakes and perhaps rodents.

Snakes, especially larger ones, feed on any animal small enough to be swallowed. Bull snakes feed on rabbits, rats and mice, birds, eggs, lizards, other snakes and toads as well as insects such as grasshoppers. The writer has found this snake feeding on or already having fed on all of the listed food articles.

Small Mammals

The population of small mammals of each of the stages in succession was determined by trapping of rats and mice, by pellet counts of rabbits and counts of dens, mounds and runs of ground squirrels, gophers and moles.

Difficulties arise when an effort is made to put all these data on a comparative basis. In order to combine all data on mammals to arrive at a figure for total populations, trap-night figures for rats and mice, pellet counts for rabbits and den, mound and run counts for ground squirrels, gophers and moles were translated into numbers from one to five, representing relative abundance for each species in each stage in succession. These figures of relative abundance were then totaled to give a figure representing relative abundance of small mammals in the various stages in succession.

Table 25 shows the number of specimens, the number of traps, the number of nights each stage was trapped and the trap-night figures for each species. This method of indicating abundance was suggested by Taylor (1930). The pellet count for rabbits in each stage was determined after the method suggested by him. These figures are also shown in Table 25. The trap-night percentage is calculated by multiplying the number of specimens by 100 and dividing this number by the number of traps times the number of nights the area was trapped.

$$\text{Trap-night percentage} = \frac{\text{number of specimens}}{\text{number of traps x number of nights traps set}} \times 100.$$

TABLE 25. THE NUMBER OF TRAPS, NIGHTS TRAPPED AND THE TOTAL CATCH OF SMALL MAMMALS IN EACH STAGE. THE TRAP-NIGHT PERCENTAGE IS ALSO SHOWN. PELLET COUNT IS RECORDED AS THE AVERAGE NUMBER OF FECAL PELLETS PER SQUARE FOOT.

Stage in succession		A	B	C	D	E	F
	Number of traps	55	45	40	70	60	55
	Number of nights	2	2	2	2	2	2
Peromyscus maniculatus bairdii:	Catch	7	4	0	0	5	4
	Trap-night	6.4	4.4	0	0	4.1	3.8
Reithrodontomys montanus griseus:	Catch	0	0	1	1	4	1
	Trap-night	0	0	1.25	.70	3.33	.90
Perognathus hispidus spilotus:	Catch	2	0	1	1	1	0
	Trap-night	1.8	0	1.25	.70	.80	0
Mus musculus musculus:	Catch	1	1	0	0	3	1
	Trap-night	.90	1.1	0	0	2.5	.90
Sigmodon hispidus texianus:	Catch	7	5	3	0	1	1
	Trap-night	6.4	5.5	3.6	0	.80	.90
Blarina brevicauda carolinensis:	Catch	0	0	0	0	0	2
	Trap-night	0	0	0	0	0	1.8
Sylvilagus floridanus alacer:	Pellet count	1.5	.25	.60	.67	.40	.15
Lepus californicus melanotus:	Pellet count	0	.08	.03	.125	.30	.15

Ground squirrels, gophers and moles were estimated as to relative abundance rather than to attempt to arrive at an absolute figure. In Table 26, the figures from Table 25 have been converted into relative abundance to correspond to figures for ground squirrels, gophers and moles.

Table 26 shows clearly the habitat preferences of the different species listed. This evidence cannot be conclusive because of the fact that only one type of succession is involved.

SOIL CHANGES

Soil samples were collected the last week in July, using a cylindrical core cutter having an inside diameter of 1.75 inches. They were taken to a depth of six inches, and several from each area. All samples from each area were combined to form a composite sample. After air drying, a mechanical analy-

TABLE 26. RELATIVE ABUNDANCE OF SMALL MAMMALS.

		A	B	C	D	E	F
Deer mice	*Peromyscus maniculatus bairdii*	5	4	0	0	4	3
Harvest mice	*Reithrodontomys montanus griseus*	0	0	1	1	3	1
Pocket mice	*Perognathus hispidus spilotus*	2	0	1	1	1	0
House mice	*Mus muscutus musculus*	1	1	0	0	2	1
Cotton rats	*Sigmodon hispidus texianus*	5	4	3	0	1	1
Shrews	*Blarina brevicauda carolinensis*	0	0	0	0	0	1
Cottontail rabbits	*Sylvilagus floridanus alacer*	5	1	3	3	2	1
Pocket gophers	*Geomys bursarius*	0	0	0	2	3	2
Jack rabbits	*Lepus californicus melanotus*	0	1	0	1	1	1
Moles	*Scalopus aquaticus*	0	0	1	2	4	3
Ground squirrels	*Citellus tridecemlineatus texensis*	0	0	0	0	1	1
Total abundance for each stage		18	11	9	10	22	15

sis by the hydrometer method, based on the procedure outlined by Bouyoucos (1936) was carried out. Forty grams of air-dried soil were placed in a dispersing chamber, 5 cc of 1 N. sodium hydroxide added as a dispersing agent and the total volume made up to 100 cc. The mixture was stirred with an electric stirrer for 15 minutes, after which 60 cc were poured into a cylinder and a hydrometer reading taken at the end of exactly 60 seconds. The seconds were measured with a General Electric Interval Timer. This reading gives density of the mixture, part of which is due to suspended silt and clay. After 14 more minutes have elapsed, a second hydrometer reading is taken. This reading shows density of the suspension after most of the silt has settled out. From the final hydrometer reading the clay content of the soil is calculated and from difference between readings is calculated the silt content. The percentage of clay and silt subtracted from 100 gives percentage of coarse sand. The terms sand, silt and clay are more or less arbitrary terms. The United States Department of Agriculture Yearbook for 1938, (page 893), defines size limits of soil particles as follows:

Sand particles—2-.05 mm. diameter
Silt particles—.05-.002 mm. diameter
Clay particles—less than .002 mm. in diameter.

In this study, the constituents are defined on the basis of time required to settle from a suspension of soil in a cylinder 6 inches high and approximately one inch in diameter.

Sand particles—settle out in 60 seconds
Silt particles—settle out in 15 minutes
Clay particles—require more than 15 minutes to settle out.

Loss on ignition was determined by two methods, first by heating weighed samples at 1200° F. for 8 hours following a preliminary drying at 105° C. for 48 hours. Losses by this method were much too high in samples con-

taining a high percentage of clay, so weighed samples (.5-.75 gm.) of oven-dried soil were heated at 240° C. for one hour, reweighed and then ignited. There was considerable difference in the amount of loss weight of samples dried at 105° C. and samples dried at 240° C. Table 27 presents data on soils. Column one indicates the areas as shown in Figure 1, the next column shows stage in succession in which each area belongs.

In column six are shown figures for the loss on combustion after drying soil at 105° C. for 48 hours. These figures are from 25 to 100 percent greater than those obtained upon igniting the soil samples after drying at 240° C. for one hour. The excessive loss is explained as due to presence of combined water. As stated by Olmstead and Smith (1938), this water can be driven off only by heating to a red heat. At 240° C., most of the combined water is driven off, although in soils having a rather high clay content and a low humus content, a considerable amount of water is retained until

TABLE 27. ANALYSIS AND COMPARISON OF SOILS FROM THE STAGES IN SUCCESSION OF ABANDONED ERODED FARMLAND TO CLIMAX PRAIRIE.

Area	Stage	% Clay	% Silt	% Sand	Combustion loss after drying at 105° C.	Combustion loss after drying at 240° C.	Check area (loss after drying at 240° C.)	% less than check	Average reduction per stage in succession	Soils group
4	A	40	24	36	7.7	4.04	4.72	....	....	Zaneis–Renfrow
41A	A	33	27	40	4.83	2.55	4.00	36	42.90	Zaneis–Renfrow
25	A	34	11	55	3.45	1.94	3.77	48	....	Windthorst–Nimrod
13	B	20	20	60	3.00	1.87	3.25	40	....	Windthorst–Nimrod
11	B	35	23	42	3.53	1.71	3.25	44	51	Windthorst–Nimrod
48B	B	11.5	3.5	85	1.28	.75	2.50	70	....	Hanceville–Conway
44	C	40	16	44	4.30	2.25	4.00	43	....	Zaneis–Renfrow
20	C	12	4	84	3.47	2.82	4.20	54	42	Hanceville–Conway
48	C	19	6	75	2.01	1.76	2.50	30	....	Hanceville–Conway
19	D	25	5	70	2.50	1.94	4.20	54	....	Hanceville–Conway
24	D	17.5	8.5	74	3.40	1.87	2.25	17	36.5	Hanceville–Conway
16	D	22	15	63	3.00	2.00	3.77	49	....	Windthorst–Nimrod
9	D	30	10	60	3.40	2.41	3.25	26	....	Windthorst–Nimrod
47	E	17	10	73	2.47	1.30	2.50	47	....	Hanceville–Conway
30	E	33	21	46	2.60	1.75	3.77	54	35.9	Windthorst–Nimrod
21	E	25	15	60	2.79	1.71	2.50	31	....	Windthorst–Nimrod
52	E	21	6	73	2.46	2.11	2.50	11.6	....	Hanceville–Conway
56	F	20	12	68	4.21	2.50	....	....	....	Hanceville–Conway
29	F	24	36	40	5.22	3.77	....	....	....	Windthorst–Nimrod
45	F	..	..	..	5.47	4.00	....	....	....	Zaneis–Renfrow
41B	F	30	28	42	3.80	3.05	....	....	....	Zaneis–Renfrow
5	F	15	33	52	5.50	4.20	....	....	....	Windthorst–Nimrod
7	F	..	..	..	5.40	4.72	....	....	....	Windthorst–Nimrod
28	F	30	22	48	4.53	3.25	....	....	....	Windthorst–Nimrod
36	F	30	22	48	5.80	3.43	....	....	....	Zaneis–Renfrow

TABLE 28. NUMBER OF SPECIES OF PLANTS PRESENT AND THE NUMBER EXCLUSIVE TO THE VARIOUS STAGES IN SUCCESSION

Stage in succession	Species present	Percent of total	Number exclusive	Percentage species present exclusive to stage represented
A (Pioneer).....	27	20.0	3	2.22
B	42	31.1	0	....
C	56	41.8	4	3.00
D	80	59.2	6	4.50
E	89	65.9	0	....
F (Climax Prairie)	94	69.6	17	12.50

a red heat is reached. It is thus explained why loss on combustion is not a reliable criterion of the humus content of soil.

TABLE 29. THE RELATIVE ABUNDANCE OF THE MORE COMMON SPECIES OF PLANTS INVOLVED IN SUCCESSION ON ABANDONED ERODED FARMLAND.

Species	STAGE IN SUCCESSION					
	A	B	C	D	E	F
Helianthus annuus	4	3	1	..	..	..
Aplopappus ciliatus	1	2	1	..	..	..
Erigeron canadensis	1	1	1	..	..	..
Aristida oligantha	1	3	5	4	1	..
Solanum carolinense	1	1	1	..	..	..
Digitaria sanguinalis	2	1	..	..	..	..
Eragrostis secundiflora	..	1	2	3	1	..
Diodia teres	..	1	1	1	..	..
Leptoloma cognatum	..	1	1	1	1	1
Plantago purshii	..	1	2	3	2	1
Cerastium brachypodum	..	3	4	3	..	..
Strophostyles umbellata	..	..	1	1	1	..
Aristida basiramea	..	..	1	3	2	..
Andropogon scoparius	..	..	..	1	3	5
Andropogon ternarius	..	..	1	2	3	..
Andropogon furcatus	..	..	..	1	1	1
Panicum scribnerianum	..	..	..	1	1	2
Erigeron ramosus	..	1	1	1	2	3
Lechea tenuifolia	..	1	1	1	1	..
Aristida purpurascens	..	..	..	1	1	1
Sporobolus cryptandrus	..	..	1	1	1	..
Petalostemon purpureum	..	..	..	..	1	1
Psoralea tenuiflora	..	..	..	..	1	1
Psoralea floribunda	..	..	..	..	1	1
Sorghastrum nutans	..	..	..	..	1	1
Sabatia campestris	..	..	1	1	..	..
Aster multiflorus	..	..	..	1	1	1
Oenothera serrulata	..	..	..	..	..	1
Bouteloua curtipendula	..	..	..	1	2	5
Achillea millefolium	..	..	..	..	1	1
Baptisia australis	..	..	..	..	..	1
Baptisia bracteata	..	..	..	..	..	1
Amorpha canescens	..	..	..	..	..	1
Panicum virgatum	..	..	..	..	1	1
Antennaria campestris	..	..	..	..	..	1
Astragalus caryocarpus	..	..	..	..	..	1

The soil of each area was checked against that of the nearest native prairie having a similar soil composition, that is, similar proportions of sand, silt and clay. The loss on ignition of check area is shown in the 8th column, with percentage difference between study area and check area in next column. The 10th column shows the average difference of all areas in each stage. These figures show the trend in humus content. Stage E, the subclimax stage, shows 36 percent less humus than climax prairie, with each succeeding stage showing less and less humus.

It is not to be expected that such a diverse group of stations should show uniform increase in humus content nor that soil constituents should check closely. According to the latest soils map, Yearbook (1938), at least three soil groups are included in the area studied.

PLANT SUCCESSION

Data taken on vegetation included relative abundance of each species during its blooming season, total density of vegetation on each area expressed as percentages of ground covered and the percentage of total vegetation contributed by the important species.

Although 140 species were recorded in the various stages of succession, most were not abundant and were classed as incidentals. Table 29 shows relative abundance and distribution of the more important plants involved in the present study.

Table 28 summarizes the distribution of the species through the stages.

As is shown, seventeen species exclusive to climax prairie were found. These are as follows:

Callirrhoe alceoides
Petalostemon multiflorus & spp.
Aster patens
Bouteloua gracilis
Baptisia australis
Astragalus caryocarpus
Vernonia baldwinii
Draba cunefolia
Agoseris cuspidata
Spiranthes vernalis
Pentstemon gracilis
Pentstemon cobea
Senecio plattensis
Engelmannia pinnatifida
Hieracium longipilium

Students of Oklahoma vegetation will immediately recognize in the foregoing list of plants some that are more or less common on prairie pastures of central Oklahoma. *Petalostemon candida, P. multiflorus, Bouteloua gracilis, Vernonia baldwinii, Agoseris cuspidata* and *Engelmannia pinnatifida* are among prairie plants that increase in abundance when prairie is grazed. Overgrazing may result in further increase in some of these and elimination from the area of others.

Of twenty-seven species listed from early stages in succession, 8 or 29.6 percent are found in climax prairie. Plants present in the pioneer stage which persist through all stages of succession including climax usually do so because of the presence of areas such as gopher mounds, buffalo wallows, sides of gullies, etc. Such plants include *Aristida oligantha, Ambrosia psilotachyia, Callirrhoe involucrata, Chrysopsis pilosa, Rudebeckia hirta*, and *Amphiachyris dracunculoides*.

As is well known by students of ecology in this region, *Amphiachyris dracunculoides* is most common on overgrazed pastures. Amphiachyris seedlings are not shade tolerant, hence the plant is rare or sometimes absent in climax prairies. Gopher mounds and diggings of other animals and areas where the soil is shallow are usually the only places in climax prairie where this plant may be found. Because of the abundance of open soil surface in pioneer stages, Amphiachyris is common here.

As is evident from Table 30, the later a species appears in the stages of succession the greater its chance of surviving in the climax prairie. The only exceptions are certain forms already discussed which survived because of the presence of small areas of bare soil in all stages of succession.

TABLE 30. NUMBER OF SPECIES OF PLANTS IN EACH STAGE OF SUCCESSION AND THE NUMBER AND PERCENTAGE SURVIVING IN CLIMAX PRAIRIE.

Stage of invasion	Number invading	Number surviving in climax prairie	Percent surviving in climax prairie
A (Pioneer)	27	8	29.6
B	18	10	5.5
C	17	10	6.0
D	29	23	79.0
E	25	24	96.0
F (Climax)	17	17	100.0

As will be noted when the table showing the number of species of insects invading each stage in succession and the number surviving in climax prairie is examined, a large percentage of the midseral insects do not appear in the climax, showing that factors other than species composition of the plant part of the community control survival of an insect in the climax association.

Nine prairie stations were selected and studied during 1938. These native prairie areas are for the most part used as hay meadows and in the fall all but two were mowed. Two stations were undisturbed, thus allowing uninterrupted study of prairie insects throughout the year. Data for the vegetation was obtained from all prairie areas. Table 31 shows the total vegetation cover and percent of the vegetation contributed by the principal

plants on the nine areas. Figures for each species have been averaged to arrive at a typical prairie vegetation.

TABLE 31. TOTAL VEGETATIVE COVER AND PERCENT OF TOTAL CONTRIBUTED BY THE PRINCIPAL SPECIES OF PLANTS ON THE PRAIRIE STATIONS.

Area number	56	29	36	45	41B	55	28	5	7	Av.	Constancy
Total vegetative cover	70	75	60	65	60	55	80	80	70	66.6	...
Andropogon scoparius	40	40	25	30	35	20	65	50	35	38.8	100
Bouteloua curtipendula	5	30	40	45	45	50	10	20	40	31.6	100
Andropogon furcatus	10	5	2	5	2	..	15	10	5	6.5	88
Bouteloua hirsuta	20	..	15	10	10	15	..	5	10	7.2	68
Sorghastrum nutans	5	3	..	1	..	..	3	1	1	1.5	68
Leptoloma cognatum	2	5	..	1	..	..	1	..	..	1.0	40
Aster multiflorus	3	4	1	2	3	6	..	..	2	2.3	76
Aristida spp.	1	2	1	1	2	2	..	1	1	1.2	88
Sporobolus asper	2	..	1	1	1	..	3	2	1	1.2	76

DISCUSSION

PLANT SUCCESSION

The vegetation of recently abandoned areas is rather heterogenous, being composed of species present on the land as weeds while it was still in cultivation and miscellaneous species which have migrated in from nearby areas and fence rows. Much land now abandoned was only half-heartedly farmed for some time previous to actual abandonment. For this reason, species of plants able to stand occasional disturbance of the soil were already established on the ground prior to abandonment. Most species of plants are prevented from occupying the soil because of changes due to erosion. Plants usually found on recently abandoned land include: *Helianthus annuus, Digitaria sanguinalis, Erigeron canadensis, Ambrosia psilostachyia, Croton texensis, C. capitatus, Aristida oligantha,* and similar plants. A reference to Table 29 showing succession of species will give some idea as to the plant complex found on recently abandoned soil.

One feature of early stages in plant succession on eroded areas is the lack of a dominant species. Another is lack of uniformity in distribution of the plants. This is due to colony development from plants already present on the areas before actual abandonment, or recently migrated into the area, and to edaphic factors produced by unequal erosion of the soil surface. This lack of uniformity often persists through most stages leading to development of a climax community. Islands of soil that have escaped the most severe erosion show more rapid development of vegetation than surrounding severely eroded soil. This is to be expected. Development from the pioneer stage is rapid at first. Many species present at time of abandonment are unable to stand

competition when not aided by agricultural operations. Invasion also occurs, leading to development of a community that is quite different from the pioneer stage. Of the plants of the initial stage, the first to be forced out is *Digitaria sanguinalis* (crabgrass), followed by Croton, Helianthus and Aplopappus. The last three mentioned may persist in very small numbers for some time, but each succeeding year finds them fewer in number and more stunted in growth. If *Aristida oligantha* was not present in the initial stage, it soon invades the area and in a few seasons completely dominates it, usually composing 95 percent of the vegetation and covering twenty to sixty percent of the soil surface.

A. Mixed Weed Stage

The first stage in succession may be called the mixed weed stage since plants present are those usually found on croplands as weeds. This stage lasts until *Aristida oligantha* assumes dominance.

B. *Aristida oligantha* consocies

The next stage may be called *Aristida oligantha* consocies. A few other species also migrate in following invasion by *Aristida oligantha* but seldom become more than locally dominant for some time. These include *Diodia teres, Chrysopsis pilosa, Chloris verticillata, Eragrostis spectabilis, Leptoloma cognatum, Monarda citriodora*, and *Xanthisima texanum*.

This stage persists a comparatively long time, depending upon physical character and amount of organic matter remaining in the soil at time of abandonment. On sandy soil where the humus content was low even before agricultural use and where the open character promoted rapid oxidation of organic matter, the Aristida stage lasts for many years, with invasion by other species taking place very slowly.

C. *Aristida oligantha—A. basiramea* consocies

In many cases it may require ten to fifteen years for enough humus to accumulate to allow establishment of *Aristida basiramea, Cerastium brachypodum* (chickweed), *Cassia chamaecrista* (partridge pea), and *Plantago purshii*, species which distinguish the third stage. Many other species now make their appearance. Most of these are not numerous but do provide food for certain insects. It is interesting to find that two species of the genus Aristida now share the dominant role. *Aristida oligantha* now has to compete for soil surface with *Aristida basiramea*, a species apparently requiring more humus in the soil before it can become established.

The two species of Aristida at this time compose from 75 to 95 percent of the total vegetation. It will be noted from Table 29 that *Aristida oligantha* shows a steady decline through all stages following its dominance in the second. The third stage, also an Aristida consocies, since one species of Aristida is still dominant, draws to a close with the increase in abundance

of *Eragrostis secundiflora,* a grass which invades this stage rather early but does not become abundant for some time.

D. Aristida—Eragrostis associes

In the fourth stage in succession on abandoned eroded farmland a number of species of plants act as seasonal dominants. They may be given subdominant ranking to distinguish them from a large number of other species which persist from earlier stages of development or which have recently invaded the community but will not become of subdominant or dominant rank until a later stage in development. These include: *Festuca octaflora, Plantago purshii, Eragrostis secundiflora, Lechea tenuifolia, Cassia chamaecrista, Andropogon saccharoides* and *Sporobolus cryptandrus.* It is interesting to note that among the minor species are found some which are dominants or subdominants of the climax community. As will be shown later, soil conditions have become much more favorable to plant growth and erosion for the most part has ceased in the fourth stage.

E. Subclimax stage

The fifth and what might be called subclimax stage is marked by a further decrease in abundance of *Aristida oligantha* and *Aristida basiramea.* These grasses now have a subdominant position. There seem to be no true dominants at this stage but rather disproportionate amounts of climax dominants. One of the outstanding features of this stage is absence of secondary species characteristic of climax prairie. Usually the dominant role is occupied by varying proportions of *Andropogon scoparius* and *Bouteloua curtipendula.* On clay soils a similar stage has the dominant role occupied by *Andropogon saccharoides* and/or *Bouteloua curtipendula.*

A large number of plants are found as subdominants in the subclimax stage. These listed represent those found upon study of a large number of areas and do not have equal rank in all areas: *Lechea tenuifolia, Aristida purpurascens, Bouteloua hirsuta, Erigeron ramosus, Sporobolus asper, S. cryptandrus, Solidago missouriensis, Aster multiflorus, Leptoloma cognatum* and *Sorghastrum nutans.*

F. Climax—*Andropogon scoparius—Bouteloua curtipendula* association

The growth habit of the dominants changes as we pass from subclimax to climax prairie. In the subclimax stage, *Andropogon scoparius, Bouteloua curtipendula,* and *Andropogon ternarius* grow as bunch grasses, with considerable distance between individual plants. The space between bunches of grass is occupied by various forbs, most of them spring annuals which complete their reproduction before the grasses resume their growth. Bunch growth-form and wide spacing are correlated with regions of the soil occu-

pied by roots. In the subclimax stage, topsoil is thin, subsoil not yet sufficiently modified to absorb water and there is only a small amount of litter on the surface to prevent evaporation. Under these conditions, the subsoil remains rather dry and grass roots tend to occupy the upper layer of soil, from which they receive the greatest benefit from rainfall. It is also well known that roots are produced more profusely in the portion of soil richest in nutrients. Because roots of grass plants in the subclimax stage occupy the surface soil for considerable distance about each plant, other plants will be prevented from being established near the grasses, at least during their growing season.

Annuals and tap root plants can compete successfully with shallow rooted plants by penetrating to deeper horizons of the soil to obtain a water supply or by growing and reproducing in spring when there is a surplus of water which cannot be used by the grass plants. Plants such as *Baptisia* spp., *Psorala* spp., *Petalostemon* spp., *Oenothera serrulata, Amorpha canescens, Astragalus caryocarpus, Liatris* spp., *Kuhnia eupatorioides, Silphium* spp., *Aster multiflorus* and *Solidago missouriensis*, send down long roots into the subsoil thus competing successfully with grasses. Plants of the genera Viola, Anemone, Nothoscordum, Allium, Claytonia, etc. complete their growth and reproduction before grasses have begun to draw heavily upon water in the top soil.

As the top soil becomes deeper, increasing the zone favorable for grass roots, the root-systems develop more downward and less outward, allowing closer spacing of the grass plants. This spacing brings about a further reduction in the numbers of plants other than dominants. This is partly due to shading and partly due to root competition. As the grass plants become more closely spaced and insolation becomes less severe, we find them branching out from the base and covering much of the soil.

Among plants which apparently require prairie soil conditions for their establishment are *Baptisia australis, Baptisia bracteata, Pentstemon grandiflora, Tradescantia occidentalis* and spp., *Astragalus caryocarpus, Petalostemon purpurea, P. candida, P. multiflorus, Senecio plattensis, Eriogonum longifolium, Liatris squarrosa,* and *Anemone caroliniana*.

It is hardly safe to say that it is prairie soil conditions which determine establishment of the species listed. Most of them are nowhere abundant and produce rather large seeds which are few in number and not favorable for dispersal unless possibly by animals. The seeds probably would be more sought after for food than the light wind-borne seeds of many species. It is interesting to note that a good many of the early invaders have easily scattered seeds. This is not so true of plants of the initial stage in succession present at time of abandonment. These plants were already scattered over the areas and the problems of dispersal was not so great.

SUCCESSION OF ANIMALS

General

Succession of species of insects as a biotic community develops may be attributed to several factors. Not all species have their presence and numbers controlled by the same factor or set of factors.

Many species of insects are specific in their food habits, feeding on only one kind or group of organisms. Such insects will not survive in a biotic community until their food plants or animals are established. Other species of insects, both predaceous and phytophagous, feed on a variety of organisms and hence show a wide successional range. Special conditions necessary for larval development control the presence of some species. Species which have larvae that feed on organic matter of soil will not survive in early stages of succession where the humus content is low. Physical conditions in a community may be unfavorable for the activities of some species. Certain Orthoptera and Hymenoptera require considerable bare soil for nest building and egg laying. Such forms are characteristic of those stages in succession in which the vegetation is relatively thin.

In addition to the factors mentioned, others must not be overlooked. Predators, parasites of egg and larva, fungous diseases, and competition for food are important factors in determining the survival of any organism in a biotic community.

Many Hymenoptera are in a sense parasitic, that is, the larvae feed in or upon bodies of other living organisms. A host may die at the onset of larval development of a parasitic hymenopteran or may live until development is completed. A good many parasitic Hymenoptera are specific in their food requirements. According to Brues (1921), specificity of parasite for host is due to physiological reaction of host tissue upon egg or larvae of the parasite.

Among the 293 species of insects listed, at least 15.5 percent are partly or wholly predaceous. This does not include a number of minor species. Many species are only occasionally predaceous. Others are predaceous in a definite portion of their life history. Coleopterans of the genus Epicauta lay their eggs in the ground near a pod of grasshopper eggs, on which the larvae feed. Adults of species of Epicauta are among the worst destroyers of cultivated plants, such as potatoes and tomatoes. These species are commonly known as plant feeders yet their larvae destroy grasshopper eggs. Including spiders, 30.4 percent of all specimens taken were predaceous wholly or in part. Table 32 shows the percentage of predators taken in each stage of succession from abandoned, eroded land to climax prairie.

TABLE 32. PERCENTAGE OF TOTAL ARTHROPODS OF EACH STAGE WHICH ARE PREDATORS.

Stage	*Percentage Predators*	*Stage*	*Percentage Predators*
A	35.7	D	27.6
B	33.1	E	29.2
C	28.4	F	23.1

As may be seen, the percentage is highest in pioneer and shows a decline in succeeding stages.

It is interesting to note that in Stage E, where, as has been pointed out, the total density of vegetation and total number of specimens of insects taken drops, there is a rise in percent of predators.

The midseral stages yield more species and specimens than the pioneer stage and more species than the climax stage. This fact is probably due to the greater variety of plant life in midseral stages and to survival of pioneer forms and invasion of climax species. Unequal erosion of soil leads to an unequal rate of recovery of plant life. In midseral stages are found small areas which recover more rapidly than surrounding, more eroded soil. Insects feeding on specific plants can make their appearance in a community as soon as their food plants appear but no sooner.

In subclimax stage E, it will be noted (see Table 2) that the number of species taken was in nearly all cases midway between the number taken in climax prairie and in midseral stages while the number of specimens shows a drop in this stage, then an increase in number in climax prairie. As has been mentioned elsewhere, this drop is correlated with the change from dominance of the soil surface by annual plants to dominance by perennial grasses. Many insects associated with annual plants of midseral stages are forced out of the community along with annual plants.

Some perennial grasses have a rather wide range of tolerance for physical and chemical conditions in the soil and thus can invade a community in rather early stages but increase in number and vigor as conditions become better suited for their growth. Thus *Andropogon scoparius* and *Sorghastrum nutans* may invade the community in midseral stages but do not reach their greatest abundance until much later.

The change in specimen/species ratio in the various stages of succession is shown in Table 33.

TABLE 33. THE SPECIMEN/SPECIES RATIO IN THE SUCCESSION STAGES.

Stage	*Ratio*	*Stage*	*Ratio*
A	13.4 + 1	D	17.1 + 1
B	16.7 + 1	E	13.0 + 1
C	18.0 + 1	F	23.9 + 1

Most species occurring in the climax are adapted to that type of habitat; thus we find species in that community reproducing more successfully than those in midseral communities where conditions are constantly changing.

In the following pages the behavior of the more prominent species of insects in succession is discussed.

Coleoptera

The best represented order of insects throughout all areas included in this study was the Coleoptera although many of the species were taken in too small numbers to indicate clearly their place in succession.

The Colorado potato beetle, *Leptinotarsa decimlineata*, was most abundant in the pioneer stages, dropping out rather rapidly as development proceeded. This chrysomelid feeds on certain members of the Solanaceae or potato family. The most common members of this family in the pioneer stages are *Solanum carolinense*, the bull nettle, and *Physalis heterophylla*, the ground cherry. The species of plants mentioned do not survive beyond midseral stages of succession and as a consequence we do not find Colorado potato beetles occurring beyond midseral stages. *Galerucella notulata* is a small dull brown indistinctly striped chrysomelid feeding chiefly on members of the genus Ambrosia, the ragweeds. Perennial ragweeds are found in all stages of succession but are most numerous in early ones. Distribution of Galerucélla is correlated with distribution of these plants. *Zygogramma exclamationis* and *Z. disrupta*, chrysomelids looking very much like their relative, the potato beetle, were collected from sunflowers and other composites throughout the growing season. *Diabrotica duodecimpunctata*, the cucumber beetle, was collected from various blooming plants, not showing much preference among different species. Adults seemed to feed on petals as well as on the softer portions of leaves. They prefer cultivated melon vines, doing considerable damage to young plants. According to Lutz (1937), larvae of these beetles live in roots of corn and other grasses, doing great damage in the southern United States. The larvae are called southern corn-root worms. These beetles appeared early in the spring and were collected even after the first frost. *Diabrotica duodecimpunctata* was collected in all stages of succession, being somewhat more numerous as the climax is approached while *D. vittata* was collected in midseral stages and in climax prairie and *D. atripennis* was collected only from climax prairie vegetation. Since the larvae feed on roots of perennial grasses, we should expect to find adults more abundant in that type of vegetation and such is the case.

A half dozen or more species of Pachybrachys were taken during this study. Most species were numerous in late stages of succession and climax prairie although one species, *Pachybrachys morosus*, a dull dusky form, was quite abundant in all stages and was collected throughout spring and summer. Its specific food plants, if any, were not ascertained. *Pachybrachys autolycus*, a yellow and black striped species was found in early stages in small numbers but was very abundant in late stages and in the climax. This species seemed to feed on a number of species of plants. The adults were taken during May, June and July. *Typophorus canellus*, a small, shiny black chrysomelid and *Luperodes varicornis*, a slender black leaf beetle with red head and thorax were very common in climax prairie in early spring. One of the flea beetles, *Phyllotreta lewisii*, was most abundant in midseral stages. Other species of the Alticidae collected include *Pleurostichus convexicaulis* in early midseral stages, *Chaetocnema denticulata* in late midseral stages, *Systena hudsonias* in midseral and climax stages and *Altica foliaceae* chiefly in climax prairie.

The larvae of all species are root feeders and play an important role in a biotic community.

Mordella melaena of the family Mordellidae is a small wedge-shaped humpbacked black beetle having its hind legs modified for jumping. Most specimens of this species were taken in the pioneer stage of succession but it was quite common in all. According to Blatchley (1910), the larvae live in pith or old wood. Some species of this genus are predaceous, feeding on various lepidopteran and dipteran larvae. Specimens of *Mordella melaena* were taken from early spring to late autumn.

Three species belonging to the Phalacridae were taken. *Phalacrus politus* was found in all midseral stages in succession but was more plentiful in early ones while *Phalacrus simplex* was captured in considerable numbers in all stages. *Phalacrus* sp. was taken in pioneer and midseral stages.

Two species of Coccinellidae or lady-bird beetles were collected in sufficient numbers to show their distribution. *Hippodamia convergens* was by far the most numerous coccinellid collected. This beetle was taken in June, July and August from all stages in succession but was much more numerous in early midseral stages. Larvae and adults of lady-bird beetles feed on aphids and are among our most valuable insect friends, aiding in the fight against aphids and scale insects. Members of this genus are collected by fruit and vegetable growers of California, put in cold storage until needed then distributed to control aphids (Lutz 1937). *Hyperaspis undulata* was taken in late midseral stages during summer and fall. Its food habits are similar to those of *Hippodamia convergens.*

Collops quadrimaculatus, a member of the Melyridae, was one of the most common of all beetles, being taken in abundance from all stages but most abundantly in midseral communities. This beetle is predaceous, both larvae and adults, and feeds on insect eggs, larvae of other insects and smaller insects. Adults were common in flowers from early spring until November.

Although the Cerambycidae or long-horn beetles are wood-borers during their larval life, adults frequent various flowers. *Tetraopes collaris* is known as the red milkweed beetle, the larvae living in the lower stems and roots of these plants. This beetle was one of the most beautiful of all collected. It was taken in midseral stages during June. *Typocerus sinuatus* was collected in considerable numbers during June and July from flower heads of *Aplopappus ciliatus* and other composites and was most common in midseral stages of succession. *Saperda populnea* was found in sunflower heads and in other flowers. Most specimens were taken in the pioneer stage. Since the vegetation of this stage contains a considerable proportion of Helianthus we would expect to get the greatest number of these beetles in this stage in succession.

The Meloidae or blister beetles were represented by nine species in the late midseral stages. The most common species was *Epicauta maculata.*

Epicauta trichrus, E. ferruginea, E. funebris and *Macrobasis immaculata* were collected from late midseral stages during June and July. All species seem to frequent flowers of many kinds and to feed on herbage. Larval history of the blister beetle is one of the most complicated encountered in the insect world. Females of Epicauta lay their eggs in regions frequented by grasshoppers. The newly hatched larva searches until a grasshopper egg-pod is found which is entered and the eggs eaten. Other members of the family undergo their development in bees' nests. The eggs are not laid in the bees' nests (Fabre, 1937), but in their vicinity. The larvae attach themselves to any hairy insect with which they come in contact. If the insect is not a bee, the larvae perish. If carried to a bee's nest, the larvae first eat the bee egg and later feed on the honey in the cell. As may be seen, the Meloidae have a rather complex relationship to the community in which they occur. Since the larvae of most species of Epicauta feed on grasshopper eggs, numerous adults might be expected in the stages where grasshoppers are the most numerous. This is indeed the case, midseral stages having the greatest number of grasshoppers and the most Meloidae. Suitable food plants for the adults also influence distribution of the species.

In another study carried on in conjunction with this one, the writer found that the number of grasshoppers was much greater in overgrazed areas than in eroded areas and that Meloidae were much more numerous in these same areas.

The numbers of blister beetles or old fashioned potato beetles sometimes reach plague proportions. The writer has seen them appear by millions in late spring, at which time they ate all vegetation in their paths. Potato and tomato patches are stripped of foliage. The beetles soon disappeared and did not appear in sufficient numbers the following year to do much damage. Adults can be driven by whipping the ground behind them with brush or pulled-up weeds. This method is used to drive them into areas surrounded by straw, after which the straw is ignited and the beetles destroyed. The sub-order Rhynchophora was represented by twenty-two species, most of which belong to the Curculionidae. Snout beetles, curculios, weevils or bill bugs live largely in fruits and seeds although certain species feed on leaves while the larvae develop in seeds and fruits. Plum curculios and cotton boll weevils are well-known representatives of the Curculionidae.

Among the more common weevils taken was *Anthonomus nigrinus,* found in buds and flowers of sunflowers and Aplopappus in June and July. It was most numerous in pioneer and rather common in climax stages in succession and was present throughout.

Mytostylus tenuis and *Taniimecus lacaena* are two rather large weevils common in late stages of succession and in the case of the first, most abundant in the climax. Food plants of these two species were not ascertained from field work or from literature, although Mytostylus seemed to occur most

frequently on *Psoralea* spp. *Cetrinus modestus* is another species most abundant in midseral stages of succession.

Mylabris obtectus, a member of the Mylabridae, is a little beetle collected in small numbers in midseral stages, most commonly in pods of *Cassia chamaecrista*, the partridge pea, although it doubtless feeds on other legumes. Its stages of greatest abundance corresponded with the stages of greatest abundance of Cassia.

Hemiptera

The Pentatomidae was one of the best represented families of Hemiptera as far as number of species is concerned. *Thyanta custator* was plentiful in all stages from pioneer to climax but was almost absent in the climax and was collected from early spring to frost. *Peribalus limbolarius* was numerous in early stages of succession in summer and fall but its greatest abundance was reached in late midseral stages. *Prionosoma podoploides* was absent in midseral stages and almost absent in the climax but was common in the pioneer stage. This is one of the few predaceous species of Pentatomidae, feeding on other insects.

The most common species of the Miridae was *Lygus pratensis,* the so-called tarnished plant bug. This species was comparatively rare in early stages and climax but very plentiful in midseral stages. *Polymerus basalis* increased in abundance from early midseral stages to climax prairie, reaching its greatest numbers in the climax while *Adelphocoris rapidus* was found in small numbers in all stages of succession but was numerous only in the climax.

Blissus leucopteris of the Lygaeidae is considered to be one of the worst enemies of sorghum and cereal crops of the United States. Much of the time the chinch bug is kept under control by its natural enemies such as Chrysops (the aphis lion), lady-bird beetles, common quail and a fungous disease produced by *Sporotrichum globiferum.* This disease spreads only during warm, moist weather, consequently the bug thrives in dry weather. Of the remaining species of Lygaeidae, *Lygaeus* sp., *Ortholomus scolopax* and *O.* sp. were most numerous in midseral stages of succession while *O. jamaicensis,* the most abundant species of the family, was found in all stages of succession, increasing in number as the climax is approached and greatly increasing in the undisturbed prairie, being the most common hemipteran in the prairie throughout the year. *Lygaeus reclivatus* occurred principally in climax prairie.

Of the total hemipteran specimens collected, *Galgupha nitiduloides* of the Corimelaenidae contributed a total of 15 percent, far more than any other species. Although common in all stages of succession, the negro bug reached its peak of abundance in midseral stages then declined somewhat in the climax, being exceeded in numbers in this stage only by *Ortholomus jamaicensis.* Negro bugs are said to feed on Plantago and other low plants.

Their distribution indicates a wide range of food plants and tolerance of soil and moisture conditions. A smaller species of negro bug, *Corimelanena quadrisignata,* was more abundant in climax than in successional communities.

An interesting predaceous hemipteran is *Phymata erosa* of the Phymatidae. Taken in July and August from midseral stages, the ambush bug was most numerous in successional stages having the greatest insect populations. This predaceous bug hides in flowers where it lies in wait to capture various insects.

Harmostes reflexulus, the only member of the Corezidae taken during this study, was very plentiful in pioneer stages, increasing in number in midseral stages, then declining to a minimum in the climax. This bug was present in all months from April through November.

The squash bug family (Coreidae) was represented by *Chariesterus antennator* which was taken in about equal numbers in all stages except the climax where few specimens were found.

A member of the Scutelleridae, *Homaemus bijugis,* was taken throughout the growing season in considerable numbers in midseral stages but was not common in climax prairie.

Orthoptera

As was shown by data, the Acrididae was by far the best represented family of Orthoptera. The most abundant orthopteran was not an acridian however. *Oecanthus nigricornis argentinus* of the Gryllidae was the most common orthopteran in all stages of succession. The tree cricket was very abundant in weedy vegetation of early stages of succession, its numbers declining toward the climax. The favorite haunt seemed to be on ragweeds and on sunflowers. This cricket was common from early spring until frost. Vestal (1913) reports that nymphs of Oecanthus feed on aphids. If they do so, aphids do not form an exclusive diet, since Oecanthus nymphs were numerous in stages where few aphids were found.

In the Acrididae, the genus Melanoplus was best represented, six species being taken. *Melanoplus differentialis* was characteristic of the pioneer stage. This species is usually plentiful in weedy vegetation and cultivated crops. Adults of *Melanoplus packardii, M. bispinosus, M. bivittatus* and *M. angustipennis* were taken in all stages and tended to be most numerous in midseral stages of succession. *M. confusus* was the most abundant species of Melanoplus and was found to be most plentiful in native prairie. This grasshopper appears early in spring and disappears by midsummer. *Syrbula admirabilis* was most abundant in the native prairie, appearing in late June and persisting until frost. This grasshopper and *Mermiria maculipennis* were found to be the ones most characteristic of the grasslands in this region. *Diapheromera veili veili* of the Phasmatidae was very common in the climax prairie but almost absent in the midseral stages and entirely absent in the pioneer stages

of succession. The phasmid is one of the characteristic prairie insects in central Oklahoma. Several egg cases of the mantis were brought into the laboratory during the fall. In the winter hymenopterans of the genus Chalcis emerged from the cases. Later on several mantis nymphs emerged from the same cases.

Acridian nymphs outnumber adults in all stages of succession. Decrease in numbers by predators and the fact that the adults are more adept at eluding capture probably accounts for most of the difference between the numbers of nymphs and adults. There may be more or less migration of adults, especially of long distance flyers such as *Schistocerca* spp.

Habitat conditions apparently improve for many Acrididae as the midseral stages are reached because the total number of specimens taken here was much greater than in earlier or later stages and the number of specimens per species was higher than in preceding or succeeding stages with the exception of the climax. Fewer species were taken in climax prairie but the average number of specimens per species was higher than in any other stage, showing that most species found in the climax are suited to that type of habitat. Soil conditions and composition of the vegetation are factors which work to eliminate certain species from the climax association. Those species requiring bare soil surface such as *Hadrotettix trifasciatus*, *Sparagemon collare*, *S. equale* and *Arphia* spp., and others are unable to maintain themselves in the native prairie except where edaphic factors permit. Species prefering coarse plants such as Helianthus, Ambrosia, *Sorghum halipense*, Aplopappus, Lactuca, *Erigeron canadensis*, and similar plants are almost entirely absent from climax prairie. These include *Melanoplus differentialis*, *Hesperotettix speciosus* and similar species.

A vast majority of Orthoptera are plant feeders and exert a direct effect upon vegetation. The most important role of these insects in the prairie biome is that of converting comparatively large quantities of plant material into animal tissues which in turn can be utilized by insect feeders such as meadowlarks, various prairie sparrows, dickcissels, various rodents, insectivores and reptiles. As far as bulk is concerned, Orthoptera probably furnish more food to insect feeders such as those mentioned than any other group of insects. Grasshoppers seem to be more universally accepted as food by birds than any other insect of the prairie. They have many predators and parasites among arthropods. Anyone who has spent any time in the field in summer has seen wasps dragging paralyzed grasshoppers to their nests. Hymenopteran families Larridae and Sphecidae are well-known hunters of Orthoptera (Rau, 1918). Spiders and mantids are frequently seen feeding on grasshoppers. Larvae of beetles of the genus Epicauta feed on grasshopper eggs and the adults were found to be the most numerous in the stages in which grasshoppers were most abundant.

Diptera

Among Diptera, the Asilidae are an interesting group. Known as assassin or robber flies, the members are predaceous both in larval and adult stages. According to Curran (1934), the size of the insect which they will eat is limited only by the ability of the intended victim to escape. A closely related family, the Therevidae, known as stiletto flies, was also represented in the writer's collections. Although only a comparatively few specimens of these two families were taken, they were reasonably abundant during summer months. These flies are very swift and usually escaped being caught in a net. They were frequently seen sitting on dead weeds, fence posts or wire feeding on captured insects. Assassin flies were most numerous in species and specimens in midseral to climax stages of succession. These insects are important in a biotic community because of their predaceous habits. The numbers of other species must be considerably reduced by their feeding activities.

A few specimens of Tachinidae were taken, though not enough to give any clue as to their successional position. Mention is made of these flies because of their parasitic larval life. The female tachinid lays her eggs on or in larvae of various insects or places it where it will be eaten by some larva or where the newly hatched larva can attach itself to some caterpillar (Comstock, 1936). In any event, the tachinid larva develops within the host larva, usually not killing it until development of the parasite has been completed. Many species of insects are parasitized. Lepidoptera, Orthoptera and Hemiptera are frequent victims. Though comparatively few in number, these flies are important in controlling the numbers of other insects. Muscids, although as a group numerous, were not as abundant as usual during the time this study was made. The Muscidae are well known through the activities of *Musca domestica*, the house fly. These flies showed no successional tendencies when considered as a group. The most abundant species was *Hylemya cilicrura*, which was present in all stages but most numerous in midseral areas. According to Lutz (1937), most members of the genus Hylemya are root and bulb feeders, sometimes doing serious damage to crops.

Very few tabanids were taken during this study. These flies are commonly known as horse or deer flies. The females do the biting, males being nectar feeders. The predaceous larvae live in water or moist earth. Specimens of Tabinidae were taken mostly in subclimax and climax stages of succession. Moisture conditions in the soil probably is the major factor in the distribution of the species. As has been pointed out, soil in early and midseral stages has a very low water holding capacity due to the low organic matter content. Such soil dries out rapidly. Soil of the climax prairie remains moist for a considerable time after each rainfall because of its high humus content and protection against evaporation afforded by the rather dense cover of vegetation.

The flesh flies (Sarcophagidae) were much more numerous in midseral stages. The larvae of most species of this family live on flesh, living or dead; some feed on decaying plant material, other parasitize snails, insects and earthworms. Certain species of sarcophagids, like the Muscidae, are often attacked by the fungus Empusa. Fungi must be considered important in the biotic community because of their effect on insects in addition to their many other roles. Bombyliidae or bee flies are of interest because of the food habits of their larvae which feed on larvae of Hymenoptera, Lepidoptera, Orthoptera and Coleoptera. The adults are nectar feeders. The number of Bombyliidae taken was too small to indicate their successional range. They were taken only in August and September.

Helomyzidae, represented by Pseudoleria, were rather common in late spring. These flies were increasingly abundant in the advanced stages of succession.

Trypanea actinobola and *Tephritis albaceps* are members of the Trypaneidae, the fruit fly family, collected during this study. These flies are important because of their effect on vegetation. Certain species cause galls to develop on goldenrod stems, larvae of other species are leaf miners, while other species live in roots and fruits (Lutz, 1937). These flies were taken throughout the growing season in early stages of succession and in the climax community. This family has received much attention because of the activities of one of its members, *Ceratitis capitata*, the Mediterranean fruit fly.

The Syrphidae or flower flies are important because of the aphid eating habits of their larvae (Lutz, 1937). *Melanostoma marginatum* and *M. melinum*, the two species taken during this study, lay their eggs in the midst of a group of aphids. The larvae feed on the juices of the aphids. These flies were uniformly distributed in all stages of succession.

Homoptera

Leaf hoppers are commonly among the most numerous organisms of the prairie. Doubtless the numbers of the various species of Homoptera fluctuate from year to year. The number of leaf hoppers in all types of habitat was less in 1938 than found in 1936 by Coyner (1938) who, using the same method as the writer, collected 2,788 specimens from normal prairie stations during 1936. Since his collections were made weekly while the collections for this study were made bi-weekly, on a comparative basis, the stations of Coyner would yield 1,394 specimens while the prairies used in the present study yielded an average of 292 specimens.

The Cicadellidae or true leaf hoppers play a very important role in grassland communities. Kellogg (1908) stated that over one million leaf hoppers can and often do live on one acre of grassland. Students of these insects estimate that leaf hoppers may destroy nearly one half of the grass appearing each year. A total of 14 species of Cicadellidae were numerous enough to

show successional trends. Table 20 shows the distribution of most species. *Driotura robusta* was abundant in pioneer stages while *Deltocephalus inimicus* was most plentiful in midseral stages of succession and *Chlorotettix unicolor, Xerophloea major* and *Thamnotettix inornatus* numerous in climax prairie.

Three species of Membracidae or tree hoppers were taken. These homopterans were the prettiest of all encountered in the prairie. *Stictocephala festina* was abundant in all stages from midseral to climax while *Vanduzea arcuata* was taken in greatest numbers in the pioneer stage and *Campylenchia latipes* was most numerous in midseral stages of succession, although quite abundant in the climax. All representatives of this family were taken from mid-spring until frost. They lay their eggs in stems of plants.

Members of the genus Scolops (Fulgoridae) are known as candle-heads or lantern flies because of the long upcurving projection borne on the anterior dorsal part of the head. *Scolops spurcus* and *Scolops* sp. were taken in all stages and seemed to be more plentiful in midseral stages of succession.

Aphrophora quadrinotata, the "spittle bug," of the Cercopidae, was conspicuous in spring because of masses of foam produced on the stems of various herbaceous plants by its nymphs. According to Kellogg (1908), the foamy spittle-like mass is produced by the "whipping" of a sticky fluid expelled from the alimentary tract of the nymph. This fluid is beaten into a froth by whisking about of the insect's body. Spittle bugs were most abundant on perennial plants such as various legumes. Adults were taken chiefly in May, June and July from midseral and climax stages and were most numerous in climax prairie.

Aphids are found on many kinds of plants but their size, body texture and location on plants do not favor collection by the sweep net method. Only a few specimens were taken during the study although they were present on many plants, especially tender annuals. Aphids can be very damaging to crops, especially when their natural controls are absent. They are important in a biotic community as food for many other insects. The feeding of ladybird beetles on aphids is well known. Various Hymenoptera and Diptera parasitize aphids and larvae of species of the Syrphidae feed on them. Certain ants feed on sugary excretions from the aphids' bodies. Ants care for them, transferring them from plant to plant, sometimes taking them under ground to roots. Aphids were most numerous in stages having a large number of plants other than grasses.

Hymenoptera

The Psammocharidae or spider wasps, like the familiar Sphecidae or mud-dauber wasps, stock their nests with spiders which serve as food for their larvae. Spider wasps dig tunnels in the ground or make cells out of mud in which they store one or more spiders and place an egg which hatches into a grub-like larva and feeds on the paralyzed spiders. These wasps were

most common in the midseral stages of succession. These same stages yield an abundance of spiders so there may be some correlation in distribution of spiders and wasps. We commonly think of spiders as wolves of the insect world yet they have their enemies.

Parasitic Braconidae were much more numerous in midseral stages, both in species and specimens than in pioneer or climax stages. These small wasps parasitize aphids and caterpillars.

Ichneumons were fairly common in all stages but were most abundant in climax and pioneer stages of succession. The females of certain species locate borers in the stems of woody plants, pierce the wood with their slender ovipositors and deposit their eggs in or near wood-boring larvae. Some species parasitize caterpillars and other insect larvae.

Members of the Chalcididae are small in size but numerous in species. Many of the chalcids are parasitic on other insects while some are gall formers on the stems of plants. Spilochalcis had more representatives than any other group. They were most abundant in pioneer and climax stages although represented in all stages of succession. According to Essig (1924), Spilochalcis is parasitic in lepidopteran and other larvae. The writer obtained specimens of Chalcis from the egg case of a mantis which was brought into the laboratory in winter.

Males of members of the Drynidae have wings while females are wingless. Mention is made of this family because the species are parasitic on Deltocephalus and Eutettix as well as other homopterans. Specimens were taken only in midseral stages of succession.

Certain species of Mutillidae are well known to barefoot boys because of the terrific sting of the wingless females. These velvet ants were taken only in midseral stages. Kellogg (1908) stated that mutillids habitually live in nests of other bees and wasps. Males of *Dasymutilla dermista* and *D. rubicosma* were collected during the study.

The Andrenidae was the best represented hymenopteran family as far as number of specimens are concerned. Although mining bees were numerous in all stages of succession, climax prairie yielded the most specimens. These bees dig tunnels in open ground where vegetation is scanty and stock their nests with balls of pollen and nectar as food for their larvae. Two factors operate to determine the distribution of these hymenopterans. Flowering plants to supply the nectar must be available and the ground must be more or less open. The perennial vegetation of advanced stages in succession is more open than early midseral stages which are characterized by a dense growth of annual grasses. Perennial plants of climax prairie supply pollen and nectar needed to stock nests of mining bees. It is of interest to note that Brooks (1923) and others found several nests of ground-nesting wasps destroyed by moles.

Large mound-building ants (Myrmicidae) in a measure control their

habitat. When a nest has been established, all vegetation for a considerable distance around the nest is cut off by the workers. These large ants prefer bare soil for starting a nest and when plants start in the nesting area, they are immediately destroyed. It is a well-known fact that old fields usually have several times as many ant dens as undisturbed areas. Ant dens in prairie regions are usually found where soil is poor and vegetation scanty, as along gullies, rocky ledges, etc. A favorite site for dens in prairie is the middle of roadways. Most mound-building ants concerned in this study were found in pioneer and midseral stages in succession. The reason for this is the large amount of bare soil surface and the comparatively short lived vegetation of these stages. *Pogonomyrmex molefaciens barbatus* and *P. m. occidentalis* were the two forms collected. Their habitats were apparently the same. Among their enemies are toads. *Bufo cognatus* and *B. woodhousii,* the common toads of prairies of central Oklahoma, have been observed by the writer and by Dr. A. N. Bragg (verbal report) to sit on ant dens and feed on the frightened occupants. Such feeding is usually done in late evenings.

Birds

Meadowlarks are usually thought of as characteristic birds of grasslands. Data obtained in the course of this study show that midseral stages in succession had a much larger population of these birds than did native prairie.

Meadowlarks continued to occupy the same areas in which they nested long after the last brood had left the nests. Young and adults of each community band together to form one large flock as fall approaches. The flock of birds continues to make the nesting area its headquarters until December or January at which time western meadowlarks *(Sturnella neglecta)* migrate into this region from the west. At this time there may be more or less migration eastward of eastern meadowlarks *(Sturnella magna magna).* Just how extensive this latter migration is is difficult to determine because of the increase in total number of larks due to arrival of birds from further west. These large flocks of meadowlarks do not obtain all their food from the nesting areas as did the nesting birds. Grainfields and barnyards are visited in search of food. When the ground is snow covered, these birds become bold enough to enter open barn doors.

Eastern meadowlarks commenced to nest in April before the last of the western species had migrated. The first nest was found April 26. A month later the young birds had left the nest. During the nesting season adult meadowlarks seemed to be constantly busy capturing grasshoppers to feed the young in the nest. Even after the young birds had left the nest, adults were seen to capture grasshoppers and feed them to the young birds. Supposedly other insects are used for food but grasshoppers seemed to constitute the chief article of diet. It is worth noting that the nesting areas were also those

found to have the largest population of grasshoppers. Examination of the nests showed them to be constructed almost entirely of shredded Aristida stems.

The dickcissel *(Spiza americana)* of the Illinois prairie was studied by Gross (1921) who found that immature birds fed largely on plant food while adults fed largely on insects. He explains this as due to lack of skill on the part of young birds. Gross estimates that the more than one million dickcissels of Illinois consume 100,000,000 insects per day.

Vesper sparrows *(Poœcetes gramineus)* feed largely on grasshoppers when these are available. Sparrows and dickcissels were not seen in the fall and winter, apparently having migrated. These species exert their greatest influence on a biotic community by feeding on insects, especially phytophagous forms such as Acrididae, during spring and summer.

Mammals

Density of the population of small mammals varies from year to year, being affected by number of predators, winter food supply, climatic conditions during season of reproduction and by disease. Rodents form the basic food supply of most of the larger predators. When their numbers decline for any reason, other animals such as insects, birds and domesticated animals are utilized for food. If small mammals or their enemies are eliminated by man, the balance between the two groups is upset.

During the fall and winter of 1938 the cotton rat *(Sigmodon hispidus texianus)* became very abundant, more so than for the past several years. Individuals in many places had difficulty in securing food. Migration of this rat into habitats normally devoid of it occurred during the fall and winter of 1938-39. In many areas included in the stages of succession of this study, rats were so abundant that adequate sampling of other species of rodents by trapping was impossible. All traps would be sprung, a good portion containing cotton rats. Mouse traps were used for the census work yet in some areas 50 percent of the traps contained rats. Areas with the highest populations of rats were among those being studied as seral stages in other types of succession and are not included in this paper.

Cotton rats usually prefer a habitat having a rather dense cover of tall vegetation such as shrubby areas along forest edges, along ravines and low areas in prairie where the grasses are extra tall and dense. As has been explained, these rats were abundant during the time this study was made and had migrated from their normal habitats into places where they are ordinarily not found. The most specimens were taken in pioneer stages, although they did not occupy these areas until the seeds and fruits of the plants growing there were mature. Few specimens were taken from midseral communities. These stages are dominated by annual grasses which do not furnish food attractive to cotton rats. Climax prairie showed a rather high

population of these animals. There was evidence of their work throughout the year in this community.

Although normally chiefly a vegetarian, cotton rats may become carnivorous and perhaps even cannibalistic when plant food runs short. Birds and their eggs often fall prey to these animals. Ground nesters such as meadowlarks and quail are especially liable to suffer. Anthony (1937) stated that like rabbits and varying hares, cotton rats have their periods of abundance and sometimes their increase assumes the proportions of a veritable plague. These rats are known as cotton rats because of their habit of harvesting cotton for its seeds.

Deer mice were more abundant in seral stages than in climax prairie while harvest mice and shrews were most abundant in climax and subclimax stages. Pocket mice seem to be confined to open soil, usually gravelly. When taken in areas where vegetation was rather dense, they were in traps that were in open spots.

Cottontail rabbits prefer an open type of vegetation where escape from enemies by running is possible. Although found in climax prairie, they are never as abundant as in more open vegetation.

The jackrabbit is usually found in short vegetation where visibility is good and running unimpeded by tall dense grass. Bunch-grass communities such as subclimax stage E, have the largest population of these animals.

Shrews were taken only in native prairie. They feed largely on insects but will eat mice and earthworms. Like moles, shrews have enormous appetites. According to Anthony (1937) they will eat twice their body weight in 24 hours and will feed on seeds if no other food is available.

Soils low in organic matter have a low population of earthworms and a correspondingly low population of moles. In stages approaching the climax, organic matter content of the soil has increased to a point where there is sufficient food to attract earthworms. In climax prairie the population of moles seems to be less than in the stage just prior to the climax. How much actual difference exists is not easily determined because of difficulty in seeing much of the soil surface in climax prairie. The comparatively stout roots of the perennial vegetation of climax prairie probably discourage extensive working by moles.

Ground squirrels were not numerous in any areas studied. These rodents prefer a short grass vegetation or a prairie with a considerable portion of soil surface occupied by *Buchloe dactyloides* and species of gramma grass. The subclimax stage offers a type of habitat somewhat like that usually occupied by these animals. The open character of the vegetation seems to be favorable to their activity. Anthony (1937) and Taylor (1930) stated that the 13-lined ground squirrel is most carnivorous of all spermophiles, as much as 46 percent of the stomach contents of this squirrel having been found to consist of animal matter, including insects (caterpillars, grasshoppers, co-

coons, insect eggs), birds, reptiles and mice. They will eat almost any flesh. Ground squirrels store seeds and grain for food.

Pocket gophers feed mainly on underground plant parts, although they may at times forage about openings to their burrows. Stages in succession in which the vegetation consists largely of short-lived annuals are not favorable to animals living on roots and rhizomes. Pocket gophers take their place in a community when the vegetation contains a considerable proportion of perennial plants. When vegetation becomes very dense, as in the prairie, the number of pocket gophers seems to be somewhat less than in more open vegetation. These animals have considerable influence upon plants of a biotic community.

FACTORS INFLUENCING SUCCESSION

Data presented in this paper show that there is a continuous change in species complex as a biotic community found on recently abandoned eroded farmland develops into a climax association. Changes in chemical composition and physical condition of the soil as succeeding generations of organisms carry on their activities and die enable new species of plants to enter and become established as a part of the community. Animals feeding on specific plants enter a community only when their host plants have invaded it. Specific feeders and parasites alike have their survival conditioned by the survival of their hosts.

The dominant species of plants of a community are those that are able to survive when all other species of plants are absent, that is, the organisms with which the dominants are associated in the community are not factors controlling the presence of dominant species of plants. Subdominants and dominants modify climatic and edaphic factors, enabling other species to survive. Influent animals feed upon dominant plants and may at times affect their growth and reproduction. Subinfluent species may be very numerous, including predators which feed upon influent animals, parasites of predators and prey and numerous phytophagous forms. Various microorganisms should not be overlooked, since disease is often more effective in decreasing the numbers of organisms than are predators.

Food for an adult animal is usually not the only factor conditioning the presence of an animal in a community. Suitable protection for eggs, food and protection for larvae and pupae as well as protection for the adults in certain cases are important factors in the survival of an insect in any habitat. Species which have predaceous larvae and phytophagous adults lead a more hazardous existence than those species which are wholly phytophagous or wholly predaceous.

Biotic succession varies with climate. The total effect of organisms and their remains is different under different climatic conditions. Drought retards decay while high temperatures hasten the process. Thus warm moist climates are not favorable for humus accumulation while low temperatures

allow organic matter to remain unchanged even though water is abundant. As has been pointed out, the rate of recovery of abandoned eroded farmland depends largely upon the rapidity with which humus is added to the soil. Thus climate is the chief factor controlling succession, soil type and climax community.

Central Oklahoma is in a region having a fairly high average temperature. This is favorable to rapid oxidation of organic matter in soil. The amount of organic matter is conditioned primarily by the amount of rainfall, since with moderate precipitation humus accumulation is favored while abundant rainfall promotes rapid decay and leaching of organic matter. Erosion removes the richest portion of soil first. As the topsoil is lost, subsoil is exposed. Ordinarily it contains a greater proportion of clay than topsoil. The increase in clay content of the subsoil is explained by the carrying downward of fine soil particles by infiltrating water and chemical weathering of sand particles of soil. As farmland erodes, plowing turns up more and more subsoil, thus the surface soil increases in clay content. When such land is abandoned, at first it will show a higher clay content than prairie; later, as clay particles are carried away in flowing water or downward by infiltrating water, the clay content becomes lower.

One of the most serious consequences of erosion is the upsetting of the colloidal balance of soil. As has been pointed out elsewhere in this paper, soil workers have found that organic colloids are intimately associated with inorganic colloids to form the important soil colloids.

Scrub oak and oak forest are able to compete successfully with grasses in moist sandy soils of Oklahoma. Alternes of scrub oak extend into the western half of the state where soil and moisture conditions are suitable, that is, an open soil, low in humus and readily absorbing and giving up water. Tongues of prairieland extend eastward on soils which contain considerable clay and are thus sufficiently compact to retard oxidation of humus and which do not yield water readily enough for growth of trees. These prairies differ somewhat in floral composition from those further west. The grasses are largely those taking water from deeper soil zones, such as *Andropogon furcatus, A. scoparius* and *Sorghastrum nutans,* with more shallow rooted plants such as *Bouteloua* spp. unable to survive in any great numbers. This is probably due to the fact that the soil, being low in humus and high in sand content, dries out quickly in the surface layers although infiltration may be rapid.

It is important to understand the various factors at work in central Oklahoma before a plan of soil conservation is attempted. The aim in restoring abandoned eroded land should be to return it to its original condition as quickly as practical using as much help from nature as possible. Much eroded land is occupied by tenants who continue their abortive agricultural efforts year to year regardless of the results. Strips of land between gullies are plowed up and down hillsides. Sometimes some crop may be planted, more

often energy or ambition is gone with plowing and erosion proceeds to take the soil loosened by the plow. Succession must start all over again on the plowed portions. It is a common sight to see a field that has been abandoned a few years being plowed. A crop is planted, fails, so the field is again abandoned. Again nature must start over.

SUMMARY AND CONCLUSIONS

(a) This study deals with floristic, faunistic and physiographic changes which occur as abandoned eroded farmland in central Oklahoma develops a covering of prairie vegetation.

(b) Quantitative study of the populations of plants and animals and soil analyses were made on a series of areas representing stages in development from recently abandoned eroded land to climax prairie.

(c) Data are presented to show that though a great number of species of plants and animals are found to be common to all stages of succession, the numbers of each species vary from stage to stage. Also many species of plants and animals were found to have a very limited successional range.

(d) Increase in humus content is only one of many soil changes which occur as the prairie community develops. It has not been possible in this study to trace all physiographic changes involved in rebuilding the soil following erosion. Other workers have found that increase in degree of aggregation of soil particles, reduction of the ease with which the soil particles are dispersed, increase in organic colloid content of the soil colloid complex and increase in water-holding capacity and ease of percolation of water are changes associated with development of a stable soil.

(e) There is some evidence that due to the open character of recently abandoned soil, its humus content may actually decrease for a few years after abandonment until the soil surface has become more or less stabilized through biotic activity.

(f) In general, animals play a secondary role in soil succession. Excreta and remains of animals may be more important for their stimulating effect upon plant growth because of certain chemical substances present in the remains than for organic matter added to the soil. More or less mechanical loosening of soil is brought about by activities of animals.

(g) The effect of insects upon plant life is complicated and difficult to interpret. Chewing, sap-withdrawal, gall formation, nectar and pollen collecting and leaf and stem mining are a few of the many activities of insects involving plant life. Every group of animals has its biological controls. Some of these interrelationships have been discussed in the text.

(h) The first plants to occupy a recently abandoned area are mostly forbs. These are replaced by annual grasses which dominate the midseral stages of succession. The annual grasses are replaced by prairie dominants as climax

conditions are approached. Perennial grasses have a bunch growth form when they first invade midseral communities. As soil conditions become more favorable and the number of perennial grass plants per unit area increases, the bunch growth form is lost by spreading of the plants vegetatively to form a sod.

(i) Midseral stages in succession show a much larger number of species of insects than climax prairies. This may be accounted for by the fact that the midseral community population of insects is made up of: (1) the majority of the pioneer stage organisms, (2) a large group of insects characteristic of midseral stages in succession, (3) most insects found in the climax are present in or invade the midseral stages. The drop in the number of species of insects in the climax stage is due to dropping out of many midseral and pioneer stage species.

(j) Rodents require both food and cover to be present in at least minimum quantities before they will occupy an habitat. If food is plentiful, an area may be occupied even though only a very small amount of cover is available or if excellent cover is present and only a small food supply available an area will be occupied by certain species of rodents. The pioneer stages, with their large-seeded species of plants such as Helianthus, Ambrosia, Croton and *Aplopappus ciliatus* offer very attractive food to many rodents even though cover is very scanty. Midseral stages, with vegetation consisting largely of annual grasses such as species of Aristida, offer very little food attractive to most rodents and a type of cover that does not seem particularly attractive to these animals. The subclimax stage, with its scattering of perennial grasses and rather abundant legumes, offers good year-around cover and a plentiful food supply; thus we find this stage showing the largest population of rodents. Although somewhat less food is available in climax prairie, excellent cover is present and a large population of rodents is found. Insectivores were found only in subclimax and climax communities, apparently being limited to stages in succession where the soil is rich and where ground dwelling insects and earthworms are abundant.

(k) Meadowlarks were found to be most abundant in midseral stages. The following factors are to be considered in explaining this: (1) low population of rodents of these stages, (2) a large population of insects, especially grasshoppers, in these stages furnishes abundant food for these birds, (3) favorable nesting sites and nesting material. Other birds characteristic of the prairie were not found nesting in any of the seral stages.

(l) Data concerning reptiles and amphibia are too meager to indicate their abundance and successional behavior.

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NOCTURNALISM—THE DEVELOPMENT OF A PROBLEM

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CONTENTS

NOCTURNALISM—THE DEVELOPMENT OF A PROBLEM

INTRODUCTION

The object of this paper is to integrate certain points of view and bodies of information into a general picture of nocturnalism. By nocturnalism is meant those general or specific activities initiated by, or enduring at night. In this report the term nocturnal refers to the night and diurnal to the day. Limiting the meaning of these two terms in this fashion avoids the confusion caused by using "diurnal" to mean both the normally illuminated portion as well as the twenty-four hour cycle.

Co-ordinated information concerning nocturnal animals has been sadly lacking in the past. Taxonomists have usually concerned themselves with an accurate diagnosis of a species' structural characteristics and usually have not recorded the time of day or night at which the form was active. Indeed, from the very nature of biological investigation, they did not possess this information. Naturalists reported sporadically the general activity period of animals, especially of birds and mammals; unless the observers were taxonomically expert in the group being observed, the activity was spoken of in very general terms indeed. Physiologists have noted the occurrence of certain functions or activities of nocturnal animals, and have described the conditions under which such internal reactions have been observed or elicited. Generally these physiological findings are part of a special problem, and too often are unknown to ecologists. Furthermore much of this information concerns common laboratory animals, under more or less unnatural surroundings, or which have their routine activities controlled or affected by man.

Within recent years several literature reviews and general accounts have appeared which have touched upon the nocturnal problem more or less closely. All of these have been timely, and have rendered the writer's task more feasible. Among these may be noted an account of the characteristics of nocturnal animals (Crawford 1934); the phenomena associated with sleep (Polimanti 1911, Fiebrig 1912, Pieron 1913, Rau and Rau 1916, Kleitman 1929); periodic physiological processes which appear to be more or less inherent in organisms (Richter 1927, Hoagland 1935, Welsh 1938).

In preparing this paper I have received the helpful criticism of three of my friends, Professors J. W. Buchanan, Alfred E. Emerson, and Karl P. Schmidt.

RHYTHMS OF THE ENVIRONMENT

Apparently certain important astro-physical forces, the natures of which are at present incompletely understood by astronomers, have induced a rhyth-

mic (as opposed to arhythmic) and dynamic (as opposed to static) environment on the earth surface. This rhythmicity is demonstrated by an almost infinite series of phenomena. For example, the sunspot cycle is rhythmic and Clements (1938) finds that this cycle can be correlated with annual rainfall. Study of the annual growth rings of trees has given evidence for cycles of climate within the last few thousand years (Huntington 1914, Douglass 1928). A great deal of information has been compiled concerning geological rhythms of erosion and deposition (Wanless 1938). Within these larger cycles are smaller rhythmic periods generally correlated as to climate with the more comprehensive rhythms, but specifically modified by latitude and having a complete cyclic character within themselves. Yearly rhythms are recognized by their seasonal meteorology on the one hand, and by recurring biological events which are to a certain extent catalogued, understood, and predictable.

In temperate regions, where the annual cycle is well defined, there are many well-known annual environmental adjustments; for example, hibernation, aestivation, and migration. Correlated with the annual rhythm of physical influences (for example, the length and amount of daylight, Park 1931, Clarke 1938), there is a definite seasonal succession of organisms within a given community (Clarke and Zinn 1937, Park 1930, Pearse 1926, Shelford 1913, Welsh 1935). Photoperiodism with particular reference to the relative lengths of day and night has been studied in relation to plant and animal adjustments to the annual cycle (Garner and Allard 1920, Kellerman 1926, Rowan 1926, Schick 1932).

Within seasonal rhythms are lunar rhythms which affect the height of tides, producing the unusually high spring tides when the pull of the sun and moon are in conjunction or opposition, and the neap tides when the moon is in its first or third quarter. Associated with these lunar tidal rhythms are rhythms of reproductive activity, the lunar periodicities of certain marine polychaetes (Lillie and Just 1913, Mayer 1908, Treadwell 1915, Pearse 1926, pp. 126-127). Thomson (1911) finds a correlation between the amount of river plankton and the phases of the moon, and freshwater rhythms are discussed by Shelford (1918, pp. 42-43). It must also be remembered that the rhythmic ebb and flow of tides is of great general importance to the marine littoral community (Keeble 1910). In some cases tidal rhythm apparently is not a causal agent, as in the lunar swarming of the prawn, *Anchistioides antiguensis*, where feeding habits and growth are important in determining periodism (Wheeler and Brown 1936).

THE NOCTURNAL ENVIRONMENT

In the preceding pages certain environmental rhythms and associated biological periodicities have been cited briefly. The twenty-four hour rhythm of day and night is of particular interest here, and must be discussed more

extensively. The most obvious and basic difference between day and night is the nearly qualitative fluctuation between light and darkness. In polar regions there is a long period of continuous illumination and an equally long period of continuous darkness; in equatorial regions day and night are quite constant in their duration throughout the year, virtually twelve hours of light and twelve hours of darkness. Between these two extremes the duration of daylight varies regularly with season and latitude.

In addition to this regular variation of daylight and darkness, daylight also varies regularly in intensity through the day and this daily march of light intensity has been measured extensively. The literature upon this measurement, and the measurement of daylight in the Chicago Area has been reviewed (Park 1931). Light intensities at dawn and dusk for clearings and forests have been given for northern Indiana (Park and Strohecker 1936). Similarly, the measurement of daylight intensity in the tropics has been reviewed, and intensities recorded in the dry season of the Panama Canal Zone by Allee (1926). Also daylight intensity in the wet season of the Panama Canal Zone has been measured (Park 1938, Park, Barden, and Williams 1940) in connection with nocturnal studies. These and numerous additional reports give a clear picture of an important factor in the twenty-four hour cycle. Many influences modify daylight intensity (Clayden 1925, Humphreys 1920, Kimball 1924, Pulling 1919, Park 1931). Consequently, there is a relatively constant absence of sunlight at night, and a regularly varying but easily modifiable daylight through the day.

Usually air temperature varies directly with daylight intensity, as does the rate of evaporation, as a rule; relative humidity varies inversely with air temperature, so that these important influences are intimately associated with light. Day is relatively variable while night is relatively constant; day may be characterized by relatively high air temperature and rate of evaporation, and relatively low humidity. Conversely night has relatively low temperature and rate of evaporation, and high humidity. This discussion of diurnal and nocturnal physical conditions is over-simplified and obvious, but has been restated here since it emphasizes the fundamental dissimilarity of the two periods of the twenty-four hour cycle, and consequently focuses attention upon the adjustments necessary for life under such a varying system.

Dawn and dusk are the two periods of the cycle when these differences become reduced; these are the periods when a far-reaching change in the activity of the great majority of animals and the green plants is initiated. These changes are of two general types, changes in the physiological activity of protoplasm, and changes in the ecological activities of the whole organism. Such changes may be directly induced by changes in the environment, or may be the result of more or less specific and deeply seated rhythms acting with, but not induced by, the varying external conditions. These phenomena will

be repeatedly discussed in the course of this article. The nocturnal environment has been described beautifully by Von Humboldt (1850, pp. 198-199) for the Orinoco rain forest and that of the British Guiana rain forest by Beebe (1925) among others, for tropical waters (Beebe 1928, pp. 75-97) and deserts (Beebe 1932). In these accounts the change from day to night is described; the importance of this change has been previously discussed in relation to tropical animals (Haviland 1926, Park 1938, Visher 1923).

Bayliss (1924, p. 548) has stated that the "whole existence of living organisms on the earth depends on the receipt of radiant energy from the sun." When it is remembered that the photosynthetic processes of plants are possible only in light, and that this essential chemical conversion takes place, therefore, during the day, the magnitude of this typically diurnal activity makes the biological differential between day and night more impressive. Day, then, becomes the period when the base of the world's food-chain is reconstituted. In general, animals are either diurnal or nocturnal, and it becomes expedient to examine nocturnal animals at this point.

THE NOCTURNAL PORTION OF A COMMUNITY

Although it has been recognized for a long time that a nocturnal fauna may be varied and numerous, no general analysis of the ecology of nocturnal animals has been made. Such desirable information is still lacking for a variety of reasons, among which the following are perhaps most significant: (1) lack of specific ecological data on the periods of activity of animals of many groups, (2) the difficulty of obtaining information concerning the activity of endoparasites, protozoans, and other types of animals under normal conditions of illumination, and (3) the planktonic forms generally must adjust to the constant pull of gravity, and consequently many adaptations to maintain stratal position may be superimposed upon the normal pattern of activity.

Despite these handicaps knowledge of nocturnality of aquatic animals and internal parasites is steadily increasing. Thus planarians are said to be more active at night than by day (Ward and Whipple 1918, p. 328); certain species of Filaria are active in the peripheral blood stream at night where they are taken up by their host mosquitoes, and are deep in the vertebrate hosts by day (Bouvier 1922, Elton 1927, Rivas 1920, pp. 409-415). Many marine annelids are active at night (Lillie and Just 1913, Mayer 1908, Polimanti 1911, Scott 1909, Treadwell 1915). Some Arbacias capture prey at night (Parker 1932) and another echinoderm, *Thyone briareus*, is reported by Stier (1933) to have the frequency of "locomotor" waves increased in number during the winter months, between 4:00 P.M. and 1:00 A.M. Polimanti (1911) found cephalopods to be more active at night in the Naples aquarium. Many crustaceans are nocturnal; for example, crayfishes (Newcombe 1929,

Roberts 1936, Turner 1926, Szymanski 1918), lobsters (Herrick 1909), crabs (*Menippe mercenaria,* cf. Boone 1930); prawns (Welsh 1935); amphipods (*Haustorius arenarius,* cf. Dennell 1933).

There is a well-known migration of plankton through twenty-four hour cycles, especially demonstrated for fresh-water crustaceans (Juday 1904, Welch 1935, pp. 226-35) and for marine crustaceans (Easterly 1919, Clarke and Zinn 1937). Information gathered by Juday (1921) shows that fly larvae *(Corethra punctipennis)* spend the day in the mud at the bottom of lakes, and rise to the surface at night. Nocturnal activity of fishes in general is greatly in need of exact investigation. Recently Spencer (1939) has made a start in this phase of the problem. A number of elasmobranchs (Polimanti 1911), conger eels, and silurids (Polimanti 1911; Forbes and Richardson 1908) are largely nocturnal. Experimental data upon the activity of tadpoles is needed. The aquatic Necturus and the giant salamander of China and Japan are nocturnal (Boulenger 1930). Among aquatic reptiles, the Crocodilia are all largely nocturnal (Regan 1937, Walls 1934), although individuals often sun themselves and may even feed by day occasionally.

The periods of activity and inactivity of amphibious and terrestrial animals are much better known than wholly aquatic species. When the large number of species already described by taxonomists is realized, and this number is compared with the number of species, the activity of which has not been recorded, it will be understood that sweeping generalizations on activity patterns are unsafe. In fact one of the functions of this paper is to emphasize the lack of even the simplest data on the problem of nocturnalism and diurnalism. In Table 1 a relatively brief digest of the predominantly nocturnal animals is presented. The animals selected are chiefly North American, and it is obvious that the contents of Table 1 could be greatly expanded. These animals are representatives of four large phyla, of which the last two, the arthropods and vertebrates, have been most carefully studied with respect to their activity. The largest class of animals, the insects, has the largest number of known nocturnal species. Again, the table does not do justice to the partially nocturnal species. For example, many normally diurnal birds (warblers, thrushes, vireos, orioles, tanagers, etc., Pearson *et al.,* 1936) migrate by night, and horses and cattle may feed at night during hot, dry weather. Extensive treatment of species which are in part nocturnal and in part diurnal would be interesting but impracticable in the present paper.

Table 1 shows that the truly social animals are not often nocturnal. The majority of the species cited are solitary, although certain of them form place aggregations at feeding grounds (Aradus, Boletotherus, Hoplocephala) or gather under loose bark (Parcoblatta, Brontes, Laemophlaeus) or form sleeping aggregations (bats), or hibernating aggregations (Crotalidae), or feed in packs. Consequently there are relatively few typically gregarious nocturnal forms, e.g. elephants, the carabid beetle, *Calathus gregarius,* and the

TABLE 1. AMPHIBIOUS AND TERRESTRIAL NOCTURNAL ANIMALS

Animal	Distribution	Authority for Data
Annelida: OLIGOCHAETA		
Earthworms	General; subterranean	Szymanski 1918, Walton 1928, Stephenson 1930, Regan 1937
Mollusca: GASTROPODA		
Terrestrial snails in general	General; vegetation	Van Cleave 1931, Boycott 1934
Anguispira alternata	Forests of Deciduous region of North America	Park, Lockett, & Myers 1931, Park and Strohecker 1936
Polygyra thyroidus	As above	Park and Strohecker 1936
Slugs in general	General; vegetation	Gerhardt 1933, 1934, Zolk 1932
Agriolimax campestris	N. A. Deciduous forests	Park and Strohecker 1936
Limax maximus	European, introduction into North America	Allard 1931a
Philomycus carolinensis	N. A. Deciduous forests	Park, Lockett, & Myers 1931
Arthropoda: Onychophora		
Peripatus and allied forms	General, discontinuous, great preponderance in rain forests	Regan 1937
DIPLOPODA		
Spirobolus marginatus	N. A. Deciduous forests	Park 1935, Park and Strohecker 1936
SCORPIONIDA	General, especially sand desert and rain forest	Regan 1937
SOLPUGIDA		
Solpugo	Arid and semi-arid areas	Schwarz 1893
ARANEIDA		Park, Barden and Williams, 1940
Amaurobius bennetti	North America	Park and Strohecker 1936
Clubiona pallens	North America	*Ibid.*
Clubiona riparia	North America	*Ibid.*
Coras medicinalis	North America	*Ibid.*
Ctenus sinuatipes	Panama rain forest	Park 1938
Ctenus w-notatus	Panama rain forest	*Ibid.*
Cupiennius foliatus	Panama rain forest	*Ibid.*
Dolomedes tenebrosus	North America	Park and Strohecker 1936
Lycosa tristani	Panama rain forest	Park 1938
Orb-weaver	India	Hingston 1920
Paradosennus nigricans	Panama Canal Zone	Park 1938
Schizocosa crassipes	North America	Park and Strohecker
Sericopelma rubronitens	Panama Canal Zone	Park 1938
Trechalea magnifica	Panama Canal Zone	Park 1938
Wala mitrata	North America	Park and Strohecker
Xysticus ferox	North America	Park and Strohecker
INSECTA (see Kennedy 1928)		
ORTHOPTERA		
Ceuthophilus latens	North America	Turner 1915, Park and Strohecker
Gryllus asimilis	North America	Lutz 1932
Gryllus domesticus	North America	Lutz 1932
Oecanthus niveus	North America	Allard 1930
Parcoblatta pennsylvanica	North America	Park and Keller 1932, Park and Strohecker
Periplaneta americana	North America	Haber 1920
Stenopelmatus	North America	Lutz 1932
HETEROPTERA		
Aradus crenatus	North America	Park and Strohecker
Aradus implanus	North America	*Ibid.*
Aradus quadrilineatus	North America	*Ibid.*
Menecles insertus	North America	*Ibid.*
NEUROPTERA		
Vermileo comstockii (larvae)	North America	Wheeler 1930
LEPIDOPTERA		
Deilephila euphorbiae		Bugnion and Popoff 1914

TABLE 1 *(Continued)*

Animal	Distribution	Authority for Data
Lasiocampa		*Ibid.*
Noctuidae	General	Brower 1930, Park and Strohecker, Stanley 1932, Williams 1935
Saturniidae	General	Bugnion and Popoff 1914
Moths (Heterocera)	Largely nocturnal	Rau and Rau 1929
COLEOPTERA		
Alobates pennsylvanica	North America	Park and Strohecker
Agathidium	North America	Park, Lockett and Myers
Amblycheila	North America	LeConte and Horn 1883, Riley Packard *et al.* 1878
Amphasia interstitialis	North America	Park and Keller
Boletotherus cornutus	North America	Park, Lockett and Myers, Park and Keller, Park and Strohecker
Brontes dubius	North America	*Ibid.*
Calathus gregarius	North America	*Ibid.*
Carabus granulatus	North America	Oertel 1924
Chlaenius aestivus	North America	Park and Strohecker
Chlaenius nemoralis	North America	Park, Lockett and Myers
Chlaenius sericeus	North America	Park and Keller
Cis fuscipes	North America	Park and Strohecker
Cleotus aphodiodes	North America	*Ibid.*
Clivinia impressifrons	North America	Park and Keller
Conosoma crassum	North America	Park, Lockett and Myers, Park and Strohecker
Cotinis nitida	North America	Hintze 1925
Dendroides bicolor	North America	Park, Lockett and Myers
Diaperis maculata	North America	Park and Strohecker
Enoclerus nigripes	North America	*Ibid.*
Erchomus ventriculus	North America	*Ibid.*
Euferonia stygica	North America	Park, Lockett and Myers
Galerita janus	North America	*Ibid.*, Park and Stohecker
Geopinus	North America	Chapman, Mickel, Parker, Miller and Kelley 1926
Glischrochilus fasciatus	North America	Park and Strohecker
Glischrochilus sanguintolentus	North America	*Ibid.*
Harpalus caliginosus	North America	Park, Lockett and Myers
Hoplocephala bicornis	North America	Park and Strohecker
Laemophlaeus fasciatus	North America	*Ibid.*
Laemophlaeus testaceus	North America	*Ibid.*
Leiodes blanchardii	North America	Park, Lockett and Myers
Leptostylus aculifer	North America	Park and Strohecker
Megalodacne heros	North America	Park, Lockett and Myers, Park and Sejba 1935, Park and Strohecker
Melanodrya striata	North America	*Ibid.*
Melanotus communis	North America	*Ibid.*
Melanotus decumanus	North America	*Ibid.*
Meracantha contracta	North America	Park, Lockett and Myers
Omus	North America	LeConte and Horn 1883
Ontholestes cingulatus	North America	Park, Lockett and Myers
Oryctes		Bugnion and Popoff 1914
Patrobus longicornis	North America	Park and Keller 1932
Penthe obliquata	North America	Park and Strohecker
Penthe pimelia	North America	*Ibid.*
Phengodes	North America	Barber 1905
Phenolia grossa	North America	Park, Lockett and Myers
Philonthus cyanipennis	North America	*Ibid.*
Photinus	North America	Mast 1912, Williams 1917, McDermott 1917, Hess 1920, Allard 1931, Rau 1932, Buck 1935, 1937, 1937a, Barnes 1919

TABLE 1 *(Continued)*

Animal	Distribution	Authority for Data
Photuris pennsylvanica	North America	McDermott 1917, Hess 1920
Phyllophaga	North America	Schwarz 1893, Forbes 1907, 1916, Davis 1916, Sanders and Fracker 1916, Park and Strohecker
Pinacodera limbata	North America	*Ibid.*
Platynus hypolithos	North America	Park, Lockett and Myers
Poecilus lucublandus	North America	Park and Keller
Promecognathus laevissimus	North America	Garnett 1920
Pterostichus adoxus	North America	Park, Lockett and Myers, Park and Strohecker
Serica parallela	North America	*Ibid.*
Serica sericea	North America	*Ibid.*
Staphylinus violaceus	North America	Park and Keller
Tenebroides corticalis	North America	Park and Stohecker
Tenebroides laticollis	North America	*Ibid.*
Tetracha	North America	Blatchley 1910
DIPTERA		
Tipuloidea	North America	Rogers 1933
	Great Britain	Robertson 1939
HYMENOPTERA		
For numerous references see		Rau 1938
Halictus galpinsiae	Panama Canal Zone	Rau 1935
Megacilissa yarrowii	Panama Canal Zone	*Ibid.*
Megacilissa matutina	Panama Canal Zone	*Ibid.*
Megacilissa exima	Panama Canal Zone	*Ibid.*
Xylocopa rufescens	Panama Canal Zone	*Ibid.*
Sphecodogastra taxana	North America	Graenicher 1911
Vertebrata: Amphibia		
SALIENTA See		Park, Barden and Williams 1940
Alytes obstetricans	Europe	Boulenger 1938
Bufo	General	Noble 1931, Crawford and Jones 1933, Boulenger 1938, Higginbotham 1939
Centrolene fleischmanni	Panama Canal Zone	Park 1938
Engystomops pustulosus	Panama Canal Zone	*Ibid.*
Hyla granosa	British Guiana	Crawford and Jones 1933
Hyla marmorata	British Guiana	*Ibid.*
Leptodactylus pentadactylus	Panama Canal Zone	Park 1938
Rana sylvatica	North America	Allen 1901
CAUDATA		
Generally nocturnal		
Plethodon cinereus	North America	Park, Lockett and Myers
Salamandra maculosa		Boulenger 1938
Triturus viridescens	North America	Pike 1886, Park, Lockett and Myers
REPTILIA		
Desert species in general. See		Klauber 1939
Arizona elegans	North America	Walls 1934
Coleonyx variegatus		Walls 1934
Crotalus cerastes	North America	Mosauer 1936
Gekkonidae (largely)	General	Noble and Bradley 1933, Walls 1934a, Regan 1937, Park 1938, Boulenger 1938
Heloderma suspectum	North America	Walls 1934
Hypsiglena ochrorhynchus	North America	*Ibid.*
Phyllorhynchus decurtatus	North America	*Ibid.*
Sphenodon punctatum	New Zealand	*Ibid.*, Regan 1937
Trimorphodon vandenburghi	North America	Walls 1934
Xantusiidae (largely)		Walls 1934a

TABLE 1 *(Continued)*

Animal	Distribution	Authority for Data
AVES		
Aegothelidae (Owlet-nightjars)	Australia, Tasmania, New Caledonia New Guinea, Moluccas	Regan 1937
Caprimulgidae (Nightjars)	World save for New Zealand and Pacific Islands	Regan 1937, Boulenger 1938, Stülken and Brüll 1938
Tinamous	Panama Canal Zone	Park 1938
Nyctibiidae (Potoos)	Tropical America	Regan 1937
Podargidae (Frogmouths)	Tropical Asia and Australia	Regan 1937
Strigiformes (Owls) largely	General	Montgomery 1899, Vanderplank 1934, Regan 1937, Boulenger 1938, Park 1938
Steatornithidae (Oil-bird)	Trinidad to Peru	Regan 1937
MAMMALIA (see Table 2)		
MONOTREMATA		
Echidnidae	Australia, Tasmania, Papua	Regan 1937, Boulenger 1938
Ornythorhynchidae		Boulenger 1938
MARSUPIALIA		
Caenolestidae (Sooty Selva)	Colombia, Ecuador	Regan
Dasyuridae (Tasmanian "Wolf")	Tasmania	*Ibid.*
(DASYURES)	Australia	*Ibid.*
Didelphyidae (Opossums)	Americas	Gregory 1936, Enders 1935, Regan 1937, Park 1938
Marmosa isthmica	Panama Canal Zone	Park, Barden and Williams 1940
Phalangeridae	Australia, Celebes, New Guinea	Regan, Boulenger
Phascolarctidae	Tasmania, Australia	Regan, Boulenger
Potoroinae (Macropodidae)	Australia	Regan
INSECTIVORA		
Shrews and Moles (generally nocturnal, but with numerous exceptions)	General	Bachman 1837, Shull 1907, Roosevelt 1910, Boulenger, Hamilton 1939
DERMOPTERA		
Cobegos (Flying Lemurs)		Boulenger
TUBULIDENTARA		
Aard Varks (Orycteropidae)	Africa	Boulenger
HYRACOIDEA		
Hyraxes (Dassies, etc.) (insufficient data for any positive statement: some species apparently nocturnal, others possibly diurnal)	Africa	Roosevelt 1910, Boulenger
EDENTATA		
Dasypus novemcinctus fenestratus	Panama Canal Zone	Park 1938
Myrmecophaga tridactyla	Central and South America	Regan
RODENTIA (could be greatly extended)		
Apodemus sylvaticus	England	Elton, Ford, Baker 1931
Arvicanthis	Africa	Roosevelt 1910
Cuniculus paca virgatus	Panama Canal Zone	Allee 1926a
Dasymus helukus	Africa	Roosevelt 1910
Dasyprocta punctata isthmica	Panama Canal Zone	Allee 1926a
Dendromys nigrofrons	Africa	Roosevelt 1910
Dipodillus harwoodii	Africa	Roosevelt 1910
Epimys (s.s.)	Africa	Roosevelt 1910
Gerbillus	Africa, Asia	Boulenger
Glaucomys volans volans	North America	Walls 1931, Gregory 1936
Graphiurus parvus	Africa	Roosevelt 1910
Hystricidae (Porcupines) and ERYTHOZONTIDAE (Porcupines)	Africa, India, Americas	Gregory 1936, Boulenger
Microtus (conflicting data on the American and British species)	North America, England	Hamilton 1937, Davis 1933, Gregory 1936, Hatfield 1935, 1940
Mus (generally nocturnal)	Africa, Europe, North America	Szymanski 1918a, Roosevelt 1910, Snell, *et al.* 1940

TABLE 1 *(Continued)*

Animal	Distribution	Authority for Data
Oenomys hypoxanthus bacchante	Africa	Roosevelt
Ondatra zibethica	North America	Gregory 1936
Peromyscus (generally nocturnal)	North America	Johnson 1926, Behney 1936, Gregory 1936, Park and Strohecker
Rattus (generally nocturnal)	General	Szymanski 1918, Richter 1922, 1927, Richter and Wang 1926, Browman 1937
Springhaas (Pedetes surdaster)	Africa	Roosevelt 1910
Tatera pothae and Tatera varia	Africa	Roosevelt 1910
Thamnomys	Africa	Roosevelt 1910
CARNIVORA		
Generally nocturnal: Felidae	General	Boulenger
African long-eared fox	Africa	Roosevelt 1910
Cryptoprocta ferox	Madagascar	Boulenger
Hyaena	Africa	Roosevelt 1910
Leopard	Africa	Roosevelt 1910
Lion (usually)	Africa	Roosevelt 1910
Lynxes	Europe, Asia, Africa, North America.	Boulenger
Skunks and Weasels (partially) (Mephitis, Mustela, etc.)	North America	Gregory 1936
Octocyon virgatus (Great-eared fox)	Africa	Roosevelt 1910
Potos flavus (Kinkajou)	Central America	Boulenger
Raccoons	North America	Schmidt 1934, Gregory 1936
Puma (usually)	Americas	Park 1938
Badgers (partially)	North America	Gregory 1936, Boulenger
Foxes (largely)	North America	Gregory 1936
UNGULATA		
Hydropotes inermis (Chinese Water Deer)	China	Boulenger
Elephas africanus (African elephant)	Africa	Roosevelt 1910
Elephants (general)	Africa, Asia	Clark 1914
Hippopotamus amphibius	Africa	Roosevelt 1910, Regan, Boulenger
Tapirs	Malay, Borneo, Sumatra, Central and South America	Regan
Tayassu pecari spiradens (White-lipped peccary)	Panama Canal Zone	Park 1938
Tragulidae (Chevrotains)	West Africa, India, East Indies, Burma, Philippines	Regan
CHIROPTERA		
Bats (generally nocturnal, with a very few exceptions; chiefly crepuscular-auroral)	General	Moffat 1905, Seton 1909, Roosevelt 1910, Warren 1910, Willey 1904, Sherman 1929, Ratcliffe 1932, Gregory 1936, Enders 1935, Borell 1937, Griffin and Welsh 1937, Boulenger 1938
LEMUROIDEA		
Aye-aye (Daubentonia madagascariensis)	Madagascar	Boulenger
Galago		Boulenger
True lemurs (largely nocturnal with a few exceptions)	Madagascar, India, Ceylon, S. E. Asia.	Boulenger
Tarsius spectrum	Malay, Celebes	Boulenger
PRIMATA		
Aotus (Night monkey)	Nicaragua to Amazon and eastern Peru	Enders 1935, Boulenger 1938

mycetophagous erotylid beetle, *Megalodacne heros*. The absence of social nocturnal animals, and scarcity of gregarious nocturnal species will be discussed later.

Nocturnal forms do not have any general feeding pattern, and the animals listed include herbivores, carnivores and omnivores. Apparently the ability to find and eat the specifically acceptable foods is not limited by the habit of nocturnalism.

Nocturnal species occur throughout the metazoan phyla which have been investigated for activity periods, and it may be concluded, therefore, that nocturnalism is a general tendency. Further, nocturnal animals are found in all basic feeding categories, are seldom gregarious and never strictly social, with the possible exception of a few ants which are said to be chiefly nocturnal.

What is the proportion of nocturnal to diurnal species in ecological communities? The answer to this question cannot be given at the present time because no one community has been thoroughly analysed with this in mind. An attempt has been made, using the mammals of two distinct areas, both of which have been studied thoroughly and the habits of the mammals observed. This comparison is presented in Table 2.

TABLE 2. COMPARISON OF THE MAMMALIAN FAUNAS OF A TEMPERATE DECIDUOUS FOREST WITH A TROPICAL RAIN FOREST REGION WITH RESPECT TO PERIOD OF ACTIVITY OF SPECIES AND SUBSPECIES

Order	CHICAGO AREA (Data from Gregory 1936)			BARRO COLORADO ISLAND, PANAMA CANAL ZONE (Data from Enders 1935)		
	Total	Diurnal	Nocturnal	Total	Diurnal	Nocturnal
Marsupialia	1	0	1	5	0	5
Insectivora	4	2	2	0	0	0
Chiroptera	7	0	7	10	0	10
Carnivora	15	0	11	9	4½	4½
Primata	0	0	0	4	3	1
Rodentia	20	12	8	16	6	10
Ungulata	2	1½	½	5	2	3
Edentata	0	0	0	5	2	3
Total, Subspecies	49	19½	29½	54	17½	36½
Total, Percentages	100	39	61	100	31	69

The most important point which emerges from this comparison (Table 2) is that the general ratio of nocturnal to diurnal species is constant for two widely different geographic areas. Further, it appears that nocturnal mammals form some two thirds, and diurnal mammals average about one third of the species under consideration. The experience of the author in these two areas has been fairly extensive and he believes that the data are reliable. The table does not include some eight species of mammals which undoubtedly roamed over the Chicago Area in the past; also there are numerous mammals

which are found in Panama, but have not been recorded from the Barro Colorado preserve. Both regions have been carefully studied by many biologists and consequently one is led to believe that these general percentages of nocturnal and diurnal components are to be expected in the great majority of mammal surveys. Whether the ratio of two-thirds nocturnal to one-third diurnal will hold for other classes of animals in these communities, or hold for the partial or total populations of different types of communities, is not definitely known. Prairies may have a higher diurnal, and sand deserts a higher nocturnal percentage, but little may be gained at this time by speculation.

Such a comparison is unsatisfactory since the analysis of only one class of animals tends to make the result faunistic rather than ecological. If the stomach contents of the carnivores among these mammals could be analysed also on the basis of activity pattern, a far more accurate picture could be obtained. Other groups are predominantly diurnal, for example, birds. Little is known regarding the activity of the myriads of mites and minute insects inhabiting the floor mold of steppe and forest. The complete activity analysis of any community food-chain, although greatly to be desired, has not yet appeared. Therefore it is not usually possible to state whether a nocturnal carnivore preys upon other nocturnal species, or whether it kills diurnal species while the latter are sleeping, or if both types of potential food are eaten in a definite ratio. Where the feeding on sleeping diurnals could be demonstrated, it might suggest a definite advantage for nocturnal carnivorism, since sleeping prey may have a raised sensory threshold.

In addition to this lack of specific and reliable information upon the activity patterns of the majority of species of animals, there are other ways in which the status of the nocturnal problem is confused and unsatisfactory. Among these is the significance of observational data upon the activity patterns of marine animals confined in aquaria as described by Polimanti (1911). Again the records of capture of insects at lights or light-traps need careful interpretation based on previous knowledge of the activity patterns of these species, since both nocturnal and diurnal animals may upon occasion come to light (Bodenheimer 1934, Cook 1930, Frost 1915, Hayward 1930, Houghton 1905, Howard 1899, Obyrne 1930, Reaumur (Bouvier 1922), Rockwood 1925, Scott 1932, Stanley 1932, and Williams 1935). Good recording light-traps, however, have been devised recently (Williams and Milne, 1935) and much better data can be expected in the future if such work is continued, for example that of Robertson (1939).

Roosevelt (1910) expressed the view that in areas where game was hunted persistently, many of the larger animals persecuted tended to become nocturnal, whereas these species were often diurnal in regions not hunted over by man.

It is also possible that the abundance or scarcity of food may alter the normal activity pattern. Environmental changes associated with change in altitude may affect the activity pattern of certain animals. Roosevelt (1910) found that the harsh-furred mouse *(Lophuromys aquilus)* of British East Africa was usually nocturnal in the lowland brush, but became diurnal in the cold, foggy uplands.

The particular weather of a given twenty-four hour cycle may affect the activity of both diurnals and nocturnals (Allard 1930, Juday 1904, Peckham and Peckham 1898, Zolk 1932). This aspect of the problem should be carefully investigated. The general picture is commonly known. Thus Park, Lockett and Myers (1931) found that many diurnal beetles (Mordellidae, Coccinellidae, anthocolous Cerambycidae) have their nightly period of inactivity on flowers or foliage prolonged on overcast days; and the strictly nocturnal rodent, the Springhaas *(Pedetes surdaster)*, may be observed to be in activity on dark days (Roosevelt 1910). The Springhaas, in common with many other rodents, lives in burrows in the soil, and further is gregarious in the inactive diurnal period. This brings to mind another question, namely, how do the diurnal occupants of deep soil burrows and other dark, diurnal inactivity niches become sensible of the gradual change from day to night, or conversely, how can sleeping nocturnals perceive through their sensory system the change between day and night? In the case of the green tiger-beetle *(Cicindela sexguttata)*, which passes the night inactive beneath the bark of fallen logs on the forest floor, temperature and changes in relative humidity may have been the determining influences (Park, Lockett and Myers 1931). Again, the sidewinding rattlesnake *(Crotalus cerastes)*, which is nocturnal but inhabits the burrows of kangaroo rats during the day, presents the same general problem, and Mosauer (1936) also finds that the stimulus causing the snake to emerge on the surface after dark is probably thermic. This is a perplexing question which requires experimentation on many animals; we will return to this general problem later in a discussion of environmentally induced versus endogenous activity. These and many other questions are awaiting analysis.

The nocturnal habit offers definite advantages. In the first place there is the performance of certain activities at night by diurnal species. Such activities would be more easily disturbed during the day, for example, the box turtle *(Terrapene carolina)* is, according to Allard (1935), diurnal save for the period of oviposition, the female laying her eggs at night. While many turtles lay their eggs by day (especially early in the morning) there are exceptions (Cutright 1940, p. 225). It is notable that the sea turtles are essentially nocturnal in their oviposition.

Again, where the constituents of a community are not all active at the same time, and are divided into regularly nocturnal and diurnal faunas, there is an obvious reduction of direct competition or overcrowding of herbivores

for food. This cleavage in activity of the community has been demonstrated (Chapman, Mickel *et al.* 1926, Carpenter 1938, Park, Lockett, and Myers 1931, Park and Strohecker 1936), and apparently is quite general for sand areas, temperate deciduous and tropical rain forests, and meadows. A cleavage in activity has been demonstrated also for large game mammals (Roosevelt 1910) and for the flight of minute insects (McClure 1938).

The carnivorous habit would be less hazardous and a similar reduction in direct competition would result if nocturnal carnivores preyed on sleeping diurnal animals, as has been suggested by Borradaile (1923), and Clark (1914), and demonstrated for certain nocturnal carabid beetles attacking sleeping butterflies by Floersheim (1906).

In addition to competition for food, there is competition for shelter. It is probably a general rule that as habitat niches increase in a series of communities, their availability is competed for directly or indirectly, and if the species population increases at the same time, niche availability would be increased by alternate occupation of the same niche by diurnal and nocturnal species. This has been demonstrated in certain cases; thus in Ceylon certain palms are used as roosts for crows at night, and fruit-eating bats occupy these roosts by day (Willey 1904).

Two additional advantages which may be mentioned here are more directly associated with the nocturnal physical environment, that is the higher relative humidity at night would tend to reduce the rate of evaporation and consequently conserve water in many forms, chiefly Peripatus, terrestrial snails, and amphibians (Crawford 1934). Second, odors may penetrate more readily, and sounds travel more rapidly, in damp air according to Crawford (1934).

It has been shown that there is a large and diversified nocturnal fauna, and that there are certain advantages in the differential distribution of activity within the community. If this is so, the large nocturnal faunas must have certain adjustments which enable them to live and multiply in their normally darkened and relatively constant environment.

ADJUSTMENTS OF NOCTURNAL ANIMALS

With a few exceptions, the adjustment of animals to nocturnalism reported thus far are morphological and physiological adaptations of the visual sense and the development of luminescent organs. In view of what has been stated previously concerning the essential differences between day and night, this is understandable. The probability must be considered that many other structural, functional and ecological adjustments are made by nocturnal species, and that investigation of this aspect of the problem will repay the necessarily sustained effort. This phase of nocturnalism has been recently reviewed (Crawford 1934) so that a detailed analysis is unnecessary. However, there are several features which need discussion.

Years ago Verrill (1897) wrote:

> Although much has been written regarding the protective and imitative colors and forms of various animals as seen by daylight, very little attention has been paid to their protective colors as seen by moonlight, twilight and starlight, when large numbers of species of small mammals and fishes, and numerous insects are most active in search of food, and most of the large carnivorous and insectivorous species are abroad in search of their prey.

The problem of protective coloration is not new, and has been discussed by biologists, pro and contra, for many years. However, within the last few years exact ecological experiments have been carried out upon mammals (Benson 1933), fishes and birds (Sumner 1934, 1935, 1935a) and upon insects (Isely 1938), the results of which show a positive protective value for certain species' coloration against their normal background coloration with respect to predation. These were largely diurnal experiments. It may be profitable, at this time, to revive Verrill's question as to the protective coloration of nocturnal animals. If precise experimental work demonstrated a positive value for nocturnal species, the problem would be greatly broadened, as well as an important adjustment for nocturnal animals added. Such an attack must be carefully planned. Not only the general objection of the protective-coloration theory must be met (Carpenter 1937, Shull 1936, 1937) but the additional problem of visual acuity and perception must be contended with. Many nocturnal species are carnivorous, and can see at night, but color vision of nocturnal animals has not been experimentally worked out and consequently, the problem remains a fruitful one. The excellent studies of Walls on nocturnal optical equipment has given a start, and experiments with such types as owls and mice, using the Sumner-Isely techniques, would be very illuminating. Nocturnal color vision must be proven by the careful quantitative pattern established by Brown (1937) for the large-mouth black bass, although such hue perception appears possible if Walls' physiological theory of the vertebrate retina is accepted (1934).

Entirely novel data have been supplied by Vanderplank (1934) which bear upon this phase of the problem. Using the tawny owl *(Strix aluco)*, Vanderplank found that at night considerable terrestrial radiation of infra-red rays was present, and postulated that the owl nocturnal vision was chiefly a utilization of infra-red radiation. This was demonstrated by experiment: living animals which served the owl for food (beetles, frogs, toads, mice and rats) all were found to emit infra-red radiation; an owl could not locate dead mice or bits of horse meat in the dark, but if these dead tissues were illuminated with infra-red rays, an owl quickly found and ate them. Hence it appears that the food of owls emit infra-red rays as a consequence of metabolism, and that the owl locates its food and sees at night by means of a nocturnal vision in which infra-red radiation is utilized. These data of Vanderplank bring an entirely new interpretation to the problem of nocturnal vision and protective coloration at night.

Finally, many animals adjust to day and night by change in color. Thus rhythmic color change, correlated with day and night, has been found in such diverse forms as crustaceans (Gamble and Keeble 1900, Menke 1911), insects (Schleip 1910), fishes (Young 1935), and toads (Slome and Hogben 1929). This phenomenon appears to be widely spread but sporadic, and found in both terrestrial and aquatic, invertebrate and vertebrate animals. The physiological nature of these periodic changes in color has been recently examined by Welsh (1938), but the nocturnal adjustment involved remains to be proven by careful investigation of color vision of predators and the protective value of the color change, before these rhythmic changes can be listed as definite adaptions for survival at night.

It is significant of the rapid and diverging growth of the general problem that quite recently Buck (1937a) found that both sexes of the firefly, *Photinus pyralis,* had a color vision extending from at least 5600 A (in the green) to at least 6900 A (deep red). Leaving this general problem for further research, there are a number of nocturnal adjustments which have been described, and certain of these are summarized in the following table (Table 3). From the examples listed, it will be noted the large number and great diversity of adjustments for nocturnal vision. In view of the general absence from the literature of parallel and numerous adjustments of other senses for nocturnalism, it appears that either the visual sense was the most easily adapted, or that the ability to see at night was of first importance to nocturnal animals. The latter is the more probable explanation.

It is quite obvious that fireflies see at night, and that they flash synchronously under certain conditions (Craig 1917, Hess 1920). Buck (1935) was able to induce this synchronous flashing experimentally, to demonstrate that vision was involved (1937), that sex attraction of males flashing in response to the flashing female was a basic causal influence, and that these females were probably acting as "leaders" (Hess, Buck) in the gathering. Therefore the luminescent organs, visual perception and mating appear to be ecologically interrelated in the fireflies. From the literature several interesting correlations can be drawn concerning these nocturnal beetles, and comparative data are given in Table 4. The information presented has been drawn from numerous studies upon the super-family Cantharoidea (Allard 1931, Balduf 1935, Barber 1905, Barnes 1919, Buck 1935, Fabre 1909, Hess 1920, Hudson 1891, McDermott 1910, 1911, 1912, 1914, 1917, Mast 1912, Williams 1917, and observations of the writer). Although the table could be greatly extended, the data presented demonstrate that the diurnal species lack photogenic organs, or possess them in a rudimentary condition while nocturnal species have photogenic organs in varying degrees of perfection. The majority of the nocturnal photurids exchange flashes between the two sexes as a definite nocturnal adjustment to mating. This presumably places a premium upon vision and ability to reach the female, and we find that the males tend

TABLE 3. ADJUSTMENTS OF NOCTURNAL ANIMALS

Nature of Adjustment	Animals Involved	Relevant Literature
Mating adaptation as a photogenic function of	Fireflies (Photuridae)	
	Chiefly *Photinus pyralis*	Buck 1937, 1937a
		Folsom 1922
		Hess 1920
Abdominal luminescence:		Mast 1912
		McDermott 1911, 1917
		Williams 1917
Thoracic luminescence:	Elateridae	Dubois 1886
	Pyrophorus noctilucus	Bouvier 1922
Nocturnal Visual Adaptations		
Invertebrates		
Periodic migration of the	Crustacea (Decapoda)	
(a) Distal (iris) pigment of compound eyes, to assume a day and a night position:	*Macrobrachium olfersii*	Welsh 1930
	Macrobrachium acanthurus	
	Palaemonetes vulgaris	Welsh 1930a
	Latreutes fucorum	Welsh 1935
	Leander tenuicornis	
	Anchistioides antiguensis	Welsh 1936
(b) Proximal (retinal) pigment	*Cambarus virilis*	Bennitt 1932a
	Latreutes fucorum	Welsh 1935
	Leander tenuicornis	
	Penaeopsis goodei	
(c) Reflecting (tapetal) pigment		Welsh 1932
	Latreutes fucorum	Welsh 1935
	Leander tenuicornis	
	Anchistioides antiguensis	Welsh 1936
	Cambarus	Welsh 1938
	Homarus	Welsh 1938
Periodic migration of the distal (iris) pigment of compound eyes, to assume a day and night position:	Insecta (Lepidoptera)	Kiesel 1894
	Plusia gamma, a noctuid moth	Demoll 1911, 1917
	Nocturnal lepidoptera	Horstmann 1935
Structure and function of the reflecting layer (tapetum); and of the several optic adjustments in general:	Insecta (General)	Comstock 1924
		Imms 1924
		Bugnion & Popoff 1914
	(Moths)	
	Sphinx	
	Bombyx	
	Deilephila euphorbiae	
	(Coleoptera)	
	Oryctes rhinoceros	
Size of facets of eye:	(Hymenoptera)	
	Nocturnal Bee	Graenicher 1911
	(Ephemerida)	
	Certain mayflies	Sharp 1918
Size of Ocelli	Nocturnal Hymenoptera	Rau 1935
Vertebrates		
Differential change in the length of rods and cones between day and night:	Pisces (Siluridae)	
	Ameiurus nebulosus	Welsh and Osborn 1937
Differential migration in the retinal pigment between day and night:	Reptilia (Crocodilia)	Laurens and Detwiler 1921
	Alligator mississippiensis	

TABLE 3 *(Continued)*

Nature of Adjustment	Animals Involved	Relevant Literature
Presence of a Tapetum lucidum: (or functional equivalent)	Pisces (Elasmobranchii in part)	Walls 1938
	Reptilia (Crocodilia)	Walls 1938t[1]
	Mammalia (General)	Hertwig 1912 Pennington 1935 Walls 1938
	(Marsupials) Opossums in general	Enders 1935 Crawford 1934 Walls 1938
	(Chiroptera) Fruit bats	Walls 1938
	(Carnivora) Many species of nocturnal cats	Walls 1938 Crawford 1934
	(Ungulata) Elephants	Walls 1938
Lens of eye Yellowish in diurnal forms as opposed to colorless in crepuscular and nocturnal forms:	Reptilia (Snakes of nocturnal habits) *Arizona elegans* *Trimorphodon vandenburghi* *Phyllorhynchus decurtatus* *Hypsiglena ochrorhynchus*	Walls 1931, 1934
	Mammalia (Nocturnal rodent) Flying Squirrels (*Glaucomys volans*)	Walls 1931
"Spectacle," a horny delamination or homologue of the palpebral complex associated with certain forms of both crawling and nocturnal habits:	Reptilia Many nocturnal snakes Lizards Gekkonidae Xantusiidae Pygopodidae	Walls 1934a
Histological structure of the retina: nocturnality associated with preponderance of rods over cones, to the pure rod retina:	Reptilia Rhynchocephalia *Sphenodon punctatum*	Walls 1934
	Lacertilia *Heloderma suspectum* *Xantusia riversiana* *Coleonyx variegatus*	
	Ophidia *Rhinocheilus lecontei* *Arizona elegans* *Trimorphodon vandenburghi* *Phyllorhynchus decurtatus* *Hypsiglena ochrorhynchus*	
	Boidae in general Viperidae in general Crotalidae in general	
	Mammalia Chiroptera (Bats)	Walls and Judd 1933 Crawford 1934
	Nocturnal Primates	Woollard 1927

[1]Walls does not cite a tapetum lucidum for birds. However the eyes of owls and nighthawks glow strongly in the beam of a night lamp, and the histology of the eyes of nocturnal birds should be investigated in this regard. Dr. Walls has recently informed me that the *lamina vitrea* is the layer which reflects light and is the functional equivalent in this respect of the tapetum lucidum in nocturnal birds.

TABLE 3 *(Continued)*

Nature of Adjustment	Animals Involved	Relevant Literature
Clear cornea	Typical nocturnal vertebrates	Walls and Judd 1933
Large eyes, absolute size or relatively to their diurnal allies:	Majority of nocturnal birds	Crawford 1934
	Nocturnal mammals	Kahmann 1930
Vertically elliptical pupil:	General	Mann 1931
	Reptilia	Mann 1931
	Rhynchocephalia	
	Sphenodon punctatum	Walls 1934
	Lacertilia	
	Xantusia riversiana	Walls 1934
	Coleonyx variegatus	
	Gekkonidae largely nocturnal	Barbour 1926 Mann 1931 Walls 1934
	Thecadactylus rapicaudus	Park 1938 Evans 1936
	Ophidia	Pope 1937
	Boidae generally	Mann 1931
	Viperidae generally	Walls 1934
	Crotalidae generally	
	Trimorphodon vandenburghi	
	Phyllorhynchus decurtatus	
	Hypsiglena ochrorhynchus	
	Crocodilia	
	Mammalia	
	Nocturnal cats in general (Many species)	
Infra-red vision	Tawny Owl (*Strix aluco*)	Vanderplank 1934

to have larger eyes and better developed powers of flight. Culmination is reached in both the phengodid and the phorurid families, in which there are apterous and larviform females with brilliant luminescence and large-eyed, winged males with generally smaller and less brilliant photogenic organs. Confirmatory evidence is found in the nocturnal bee *(Sphecodogastra texana)*, where the pollen is gathered from flowers from after sunset until ten o'clock at night. Females of this bee are flightless and have normal eyes, whereas the males are good night flyers and large facets characterize their eyes (Graenicher 1911). Again, in the photurid *(Pyropyga fenestralis)* the adults are diurnal and lack functional photogenic organs, while the carnivorous larvae are nocturnal and possess well-developed luminescent powers. The possession of photogenic organs by photurid larvae requires further investigation as to its significance.

Courtship, fighting patterns and other aspects of behavior have been correlated with nocturnality of geckos (Noble and Bradley 1933, Evans 1936) so that mating behavior and nocturnalism offer research opportunity with vertebrate as well as invertebrate animals.

TABLE 4. CORRELATION OF CERTAIN PHYSIOLOGICAL AND ECOLOGICAL FUNCTIONS IN CANTHAROID BEETLES

Taxonomic Group	Activity	Feeding	Luminescence		Wings	
			Male	Female	Male	Female
I. CANTHARIDAE...	Diurnal (Adults)	Carnivorous and Herbivorous	Absent	Absent	Present	Usually present
II. LYCIDAE.........	Diurnal	Herbivorous (Larvae xylophagous)	Absent	Absent	Present	Present or larviform and apterous
III. DRILIDAE........ Drilus Malacogaster	Diurnal?	Adults? Larvae feed on snails	Absent	Absent	Present	Larviform and apterous
IV. PHENGODIDAE... Phengodes Zarhipis	Nocturnal	Carnivorous	Absent	Present	Present	Larviform and apterous
V. PHOTURIDAE..... (Lampyridae, s.s.)		(Larvae feed chiefly on snails)				

DETAILS OF ADULT PHOTURIDS

	Activity	Female		Male	
		Metawings	Luminescent Organs	Metawings	Luminescent Organs
Pyropyga fenestralis............	Diurnal	Present	Absent	Present	Absent
(larvae...............	Nocturnal	Absent	Present	Absent	Present)
Ellychnia corrusca..............	Diurnal	Present	Vestigial	Present	Vestigial
Lucidota atra..................	Chiefly diurnal	Present	Poorly developed	Present	Poorly developed
Photuris pennsylvanica..........	Nocturnal	Present	Present	Present	Present
Photinus consanguineus pyralis marginellus, etc. Pyractomena Luciola lusitanica	Nocturnal	Present, but fly seldom; (P. castus only crawls)	Present, usually average smaller than males	Present, fly very well as a rule	Present, usually average larger than females
Lampyris noctiluca Pelania mauritanica Microphotus angustatus Phausis Phosphaenus hemipterus Lamprophorus tenebrosus	Nocturnal	Highly vestigial or wholly absent	Present, usually average larger than males	Present	Present, usually average smaller than females

Although the nocturnality of bats has long been known, and their marked agility in the air has been substantiated, the recent observations of Borell (1937) appear to necessitate further research upon the adjustments of these usually nocturnal forms in their nightly search for food. Borell found that bats could be easily obtained by stretching wires over a water tank, when the

bats coming in, presumably to drink, were unable to avoid the wires and fell into the water!

Even such generally adjusted forms as men, which are essentially neither diurnal nor nocturnal in the strict sense of the word, have some adjustment for nocturnal conditions, as has been shown by Cobb (1923, 1923a) in a study of dark adaptation with reference to night flying of aeroplanes.

Before turning to the subject of nocturnal activity *per se*, there is a very important biological adjustment which must be examined briefly.

SLEEP OR ITS PHYSIOLOGICAL EQUIVALENT

Although certain animals are reported in more or less continuous activity, as are larvae of the noctuid moth, *Anticarsia gematilis* (Watson 1916) and the oyster (Nelson 1921), others are said to be normally active for only a small fraction of the twenty-four hour period, as are certain Phasmidae (Annandale 1902, Schmidt 1919). The majority of metazoans have more or less regular periods of activity and recuperation. Generally these periods alternate rhythmically under normal conditions, following a species pattern with individual variation. The necessity for protoplasmic rehabilitation following photoplasmic activity is a thoroughly grounded physiological principle, and similarly activity of the organism, in its search for food, must be followed by inactivity and rest.

In a discussion already too long, the author does not propose to review the literature upon sleep. This has been done by numerous investigators (Polimanti 1911, Werner 1911, Fiebrig 1912, Pieron 1913, Rau and Rau 1916, Rau 1938, Kleitman 1929, Park, Lockett, and Myers 1931, Laird and Muller 1930). The unsatisfactory state of information upon sleep must be reaffirmed. It is especially unsatisfactory with regard to a general theory which will explain sleep of organisms as a whole. The long continued and brilliant attack upon the physiology of mammalian sleep by Kleitman and his co-workers (Kleitman 1923, 1925, 1928, 1929, 1932, 1933, 1933a, 1937, 1939, Lee and Kleitman 1923, Reed and Kleitman 1925) has given a precise experimental picture of recuperation in dogs and men; their results should apply, in general, to higher vertebrates. Conklin (1927), Laird and Muller (1930), and Freeman (1935) have, with others, studied sleep in man from a psychological point of view. Conklin summarizes:

> Sleep may be said to be an instinctive mechanism with its own special neuron pattern activated by a great variety of stimuli, according to the experience of the individual. It is facilitated by relaxation and reduction in the number and strength of sensory stimuli as well as by the presence of limited amounts of fatigue substances in the body.

Pieron (1913) finds that sleep is a suspension of those sensory-motor activities which bring the individual into relation with its environment, and which

is accompanied by a characteristic diminution of muscle tonus, loss of equilibration, reduction of spontaneous activity, elevating the threshold of irritability, and absence of critical reactivity. Kleitman (1933) found sleep to be a habit depending upon the cerebral cortex for its development, demonstrated by his previous work on decorticated dogs, and states that the twenty-four hour variation in sleep and activity of the organism is one of several periodic variations which show a twenty-four hour rhythm; further, Kleitman views the sum total of these rhythmic variations, including sleep and activity, as manifestations of a twenty-four hour rhythm in organisms which have adjusted their lives to the alternation of day and night. He finds in man a diurnal variation of speed and accuracy of performance, and a variation in body temperature and excretion of phosphates. These day-night variations he finds may be a consequence of a diurnal-nocturnal rhythm in tonicity of the skeletal musculature, and the latter variation is held to be probably responsible for the development and persistence of the sleep habit.

Kleitman (1929) in a theoretical and summarizing paper found sleep to be an easily reversible inactivity of the cerebral cortex due to a break between the cortex and other parts of the nervous system, this break resulting from a marked decrease in the number of afferent impulses. He believes that sleep is due to fatigue of the neuro-muscular mechanism concerned in the maintenance of muscular tonus. In this theory of sleep, Kleitman excludes hypnosis, narcosis, and coma.

Now when an examination of the literature upon sleep in insects is made, it is found that many insects, especially in the order Hymenoptera, have a normal inactive period characterized by a marked rigidity. In fact, many are inactive, with their legs and body rigid, and grasping a twig, leaf or stem by the mandibles alone (cf. literature cited by Rau and Rau 1916, and Rau 1938). Other insects do not have this rigid inactive condition.

Fiebrig (1912) in a critical review, compared insect sleep with sleep of vertebrates and found both groups have in common (1) relative inactivity while asleep, (2) raised threshold of irritability among other resemblances; but the rigid condition of the insect muscles, while asleep, he held to be analagous to the condition of humans when under hypnosis. Pieron (1913) went further in that he separated sleep of invertebrates and even some fishes from the sleep of mammals, regarding the sleep of the former to be nothing more than comparative immobility depending upon external influences.

When the many theories of sleep are considered, a number of which have been discredited, we are impressed with, first of all, a lack of agreement upon what sleep consists of. Thus sleep is instinctive according to some and habitual according to others; it is rigidly limited to the very highest vertebrates, or a general response. Some years ago at a symposium on sleep at the Biology Club of the University of Chicago, the material presented was confined to such mammals as dogs and men. In the discussion which fol-

lowed on sleep in general, the physiologist Ralph Lillie stated that at least we could consider sleep in the broad sense as a general anesthesia. This is one of the very few general ideas concerning sleep that have come to the author's attention.

The word "sleep" appears to include a considerable variety of physiological states which may not be comparable. My own position is that we do not gain by limiting sleep to mammals until the problem has been experimentally exhausted, and the problem will not be exhausted by working only with one group of animals. Rather we must attack the rigid sleep of certain insects by the same refined physiological techniques employed with mammals, and review or investigate the inactive states of animals from protozoans to higher vertebrates. Again, how is rigid insect sleep to be understood by comparing it with death-feigning (letisimulation) of insects or hypnosis of other animals if letisimulation and hypnosis are not thoroughly understood. Recent data by Payne (1937) on death-feigning in insects should be followed up by an extensive and intensive exploration of insect sleep.

Finally, we should note that protoplasm is a labile and dynamic system, highly irritable, highly specific but having certain general properties. Activity followed by inactivity may be looked upon as a general protoplasmic phenomenon, and recuperation of the body as a whole would seem to be inactivity at a quantitatively different level of organization. Naturally, as the organism becomes more complex, the pattern of sleep will change but if it is said that mammalian sleep differs qualitatively from, say, insect sleep, then must we not say that mammalian activity, and consequently muscle physiology, is also unrelated in the two groups? We are hardly in a position to say this at the present time, and when nocturnal activity is discussed in the following pages it should be kept in mind that inactivity is a normal correlative of activity.

ENVIRONMENT AND ACTIVITY

Since irritability is a quality of protoplasm we would expect the dynamic environment to elicit a wide variety of protoplasmic responses. This is substantiated by the large literature upon behavior (Jennings 1906, Loeb 1918, Mast 1911). However, since periodism is to be discussed presently, certain environmental stimuli must be spoken of at this time. Some of these have been noted previously, for example lunar periodicity and the relative length of the day and the night. Other effects are so thoroughly known that not more than passing reference is necessary, viz. the involved relation of radiant energy to the endocrine and sexual cycle of birds and mammals (cf. J. Benoit, T. H. Bissonnette, L. G. Browman, E. W. Dempsey, M. Hill, F. H. A. Marshall, C. R. Moore, W. Rowan and others).

In the previous review of nocturnal animals the effect of local weather upon species activity was discussed. In this discussion light intensity ap-

peared to be an important influence in these and many similar observations. The nocturnal activity of the wood mouse *(Apodemus sylvaticus)* is partially controlled by light (Elton, Ford, and Baker 1931); the diurnal wren *(Troglodytes musculus)* and diurnal bees *(Trigona mosquito)* of the Panama Canal Zone were shown by Lutz (1931) to have their activity pattern partially modifiable by light intensity. In polar regions where, save for the spring and autumnal periods, there are long continuous stretches of darkness or light, the influence of light is less obvious. Elton (1927) finds that the species of polar areas are largely diurnal animals and Hesse (1924) states that bees work in the illuminated arctic period. Pearse (1926) notes that polar Eskimos have highly irregular periods of activity and recuperation.

Under laboratory conditions of continuous illumination, Warren and Scott (1936) found that hens lay continuously, whereas eggs are laid only in daytime under normal alternation of day and night.

Generally light and temperature operate together under normal conditions; their effects are partially compound and must be carefully separated. Chapman (1923) found that the leaf-mining beetle *(Taphrocerus gracilis)* was positive to light at high field temperatures, flying when stimulated, whereas the species became negative to light at low field temperatures and upon stimulation folded the appendages and fell to the ground or into the axils of the leaves where they were inactive. In the laboratory under controlled conditions, Chapman found that the beetles could be brought into the light by increasing the temperature and made to retire by lowering the temperature. Their response to light and temperature, then, regulates their twenty-four hour activity cycle, and affords an excellent example of environmental control of poikilothermal forms.

Chapman and co-workers (1926) carefully studied the daily emergence and activity of a number of insects forming part of a Minnesota sand dune community and found that the night sand fauna differed from the day sand fauna, the change in activity of the inhabitants being closely correlated with change in temperature; similarly Park and co-workers (1931) found an apparent correlation between the rhythmic change in temperature, light, relative humidity and rate of evaporation and the change in activity of diurnal and nocturnal animals of an Ohio beech-maple forest community.

Body temperature is obviously correlated with air temperature in poikilothermal species and temperature is an important influence of animal activity. Simpson and Galbraith (1905) and Wetmore (1921) found that normally diurnal birds and normally nocturnal birds had opposite body temperature curves, the body temperature of each type coinciding with the periods of rest and activity. Hilden and Stenbäck (1916) confined birds in a dark room and regulated their activity by artificial illumination. By this technique they were able to reverse the body temperature rhythm. The importance of temperature with regard to reptile activity has been demonstrated by Mosauer

(1936), and is being pursued, notably by Raymond B. Cowles at Los Angeles.

Moisture is well established as a critical environmental influence; the enormous literature is ably summarized elsewhere (Chapman 1926, Elton 1927, Shelford 1913). Boycott (1934) found that relative humidity was influential in determining field activity of snails, and Rogers (1933) states that crane-flies (Tipuloidea) are nocturnal or crepuscular but believes this to be a response to a favorable ratio between humidity and rate of evaporation. Shelford (1914, 1914a) has previously demonstrated the rate of evaporation to be of great importance in regulation of activity and Necheles (1927) found that a relative humidity of between 75 percent and 85 percent was favorable for the activity of mosquitoes, these animals retiring during the day to avoid the low humidity and high rate of evaporation.

It is abundantly demonstrated, therefore, that changes in the environment effect changes in activity, and since the larger environmental changes are rhythmic in nature it follows that a more or less rhythmic activity would result. The literature cited, however, has been concerned chiefly with study of activity through observation or indirect measurement. Direct recording of activity was studied first by Stewart (1898), Slonaker (1908, 1912) and by Szymanski (1914). Using various types of recording machines, Szymanski found (1918c) that the blow fly *(Calliphora)* was diurnal and monophasic, e.g. that the flies exhibited a major recuperative period at night and a major activity period at day; that crayfish were nocturnal and monophasic in general, the greatest activity coming between seven and nine o'clock in the evening; that earthworms were nocturnal and polyphasic, showing about four rest and four activity periods in the twenty-four hour cycle with the greatest activity falling between two o'clock in the afternoon and midnight, and that the earthworms were active about fourteen hours out of the twenty-four. He found that snails had an uneven distribution of rest and activity periods; rabbits were polyphasic, being active for about twelve hours of the twenty-four hour cycle, with from sixteen to twenty-one activity and rest periods; the domestic cat had relatively unbroken sleep at night, and a few relatively active periods at day, and this monophasic diurnality he regarded as being secondarily imposed upon it by the sleep-activity pattern of man. Szymanski (1918a) also studied white rats and found that they were typically polyphasic, with a general nocturnal tendency, and an activity of about ten hours out of the twenty-four; in the same paper he found that waltzing mice were also polyphasic, generally nocturnal, and active some fourteen hours out of the twenty-four hour cycle. Later he investigated the activity of human infants (1918b) and of men (1922); these studies will be discussed later.

When the writer (Park, Lockett, and Myers 1931) had completed the survey of a forest community at night, and found a striking coincidence between the activity and the operating environmental influences, it was realized that only the parallelism of environmental and animal activities had been

demonstrated, and if this relationship was to be further analysed, constant environmental conditions must be obtained. Consequently, a study of typical forest species under controlled surroundings was initiated to throw light upon this parallelism (Park and Keller 1932). The first species used was the common forest cockroach *(Parcoblatta pennsylvanica)*, and it was found that this species tended to give maximal activity until fatigued, when held in total darkness and constant air temperature and rate of evaporation.

Recently Nielsen (1938) has studied the activity and song of three katydids *(Tettigonia viridissima, T. cantans,* and *Decticus verrucivorus)* by means of recording equipment. Nielsen was able to demonstrate that the activity, and to a less extent the song, was largely induced by regulation of the illumination, and in constant darkness no clear rhythm persisted. Here, as in Chapman's study with *Taphrocerus gracilis* (1923) and the forest roach, the data supported the already heavily documented conclusion that environment controlled activity and induced periodicity in many species. Other data were to follow shortly, however, to broaden the activity concept.

Although it is not safe to generalize very far, since each species of animal apparently has a specific set of physiological requirements and activity pattern, those activity patterns which are wholly or in great part regulated and induced by the rhythmic twenty-four hour day-night cycle, may be called the Exogenous Type of Activity. This is a general and collective concept, the precise limits of which are not yet defined (Park 1940a).

PERIODISM AND ACTIVITY

Not all animals have their activity so easily controlled; rather the pattern is more deeply seated, more or less regulated internally, and under constant experimental conditions tends to continue its rhythmic character. When the author was working with the forest cockroach, *Parcoblatta pennsylvanica,* he also was studying the activity of a forest fungus beetle, *Boletotherus cornutus.* This beetle is nocturnal, feeds upon fungi, especially shelf fungi (Fomes), copulates and oviposits on the fungus, and the larvae develop and pupate within the fungus. This beetle, when placed under identical conditions as the forest roach, namely total darkness, constant temperature, and constant rate of evaporation, continued to exhibit its normal nocturnal activity and diurnal inactivity. In other words, under constant conditions its activity was periodic. This is but a single example of rhythmic behavior, and a number of similar instances have been reported in recent years as given in the following table (Table 5).

From Table 5 it will be seen that periodic activity, under constant environmental conditions, has been demonstrated by investigators, working in widely separated localities, and upon a variety of animals. These animals embrace laboratory and wild stocks; individuals of both sexes, of various ages; both

TABLE 5. PERIODIC ACTIVITY OF ANIMALS UNDER CONSTANT CONDITIONS

Chronology	Animals Involved	Conditions	Literature
1917–1919	Copepoda (Acartia)	Vertical migration in constant darkness	Esterly (contra Franz, 1911-1913)
1918	White Rat	Constant darkness	Szymanski
1922	White Rat	Constant darkness	Richter
1925	*Cotinis nitida* (Larvae)	Constant darkness and constant light	Hintze
1926	*Peromyscus leucopus*	Constant darkness	Johnson
1930	Japanese Waltzing Mouse	Constant darkness	Wolf
1932	*Boletotherus cornutus*	Constant darkness	Park & Keller
1932	Stenopelmatus	Constant darkness	Lutz
1932	*Gryllus domesticus*	Constant darkness	Lutz
1932	*Gryllus assimilis*	Constant darkness	Lutz
1933	*Thyone briareus*	Constant dim red light	Stier
1933	Microtus	Constant darkness	Davis
1935	*Megalodacne heros*	Constant darkness	Park & Sejba
1935	*Spirobolus marginatus*	Constant darkness	Park
1936	*Huro salmoides*	Oxygen consumption in constant dark	Clausen
1936	*Ameiurus melas*	Oxygen consumption in constant dark	Clausen
1936	White Rat	Constant darkness	Browman
1937	*Myotis lucifugus*	Constant darkness	Griffin & Welsh
1937	*Pipistrellus subflavus*	Constant darkness	Griffin & Welsh
1939	*Bufo americanus*	Constant darkness and constant light	Higginbotham
1939	*Bufo fowleri*	Constant darkness and constant light	Higginbotham
1939	Peromyscus	Constant light	Johnson

larvae and adults. The list includes holothurians, copepods, crickets, beetles, fishes, toads, mice, rats and bats. In certain experiments the constant conditions maintained are not sufficiently rigid to withstand criticism, but in the majority of cases light intensity was constant or constant darkness was complete, and air temperature, relative humidity and rate of evaporation were controlled.

Therefore such periodism appears to be a general response which is repeated under abnormally constant conditions. This rhythmicity is quite different from environmentally induced periodism in that the former deeply seated periodism has been shown to persist under constant conditions for from a few days in some species, to over eighteen months in others.

In order to obtain objective data on periodism, at least two essential conditions must be met. First, the animals must be under constant environmental conditions (which immediately introduces an abnormal factor since most species inhabit periodic environments). Second, recording apparatus should be used. Within recent years recording equipment has been devised. Apparatus for larger terrestrial animals (rats, mice, toads, bats), utilizing elastic bands, springs, excentric drives has been reported, sometimes incompletely (Slonaker 1908, 1912, Szymanski 1918, Richter 1922, Richter and Wang 1926, Davis 1933, Colton 1933, Durant 1935, Browman 1936, Hemmingsen and Krarup 1937, Griffin and Welsh 1937, Park 1938, Higginbotham 1939, Park and Woods 1940); for small terrestrial animals (crickets, grasshoppers, beetles) by Lutz (1932), Park (1935) and Nielsen (1938); for aquatic species (crayfish, fishes) by Spencer (1929) and Park, Roberts

and Harris (1940); and within recent years sound-recording apparatus based on the audio-frequency principle (Park 1937, Nielsen 1938) and other electrical devices (Kendeigh and Baldwin 1936, Spencer 1939, Odum and Kendeigh 1940). It is apparent that technical difficulties are being overcome.

There are other difficulties, more human and consequently less easily corrected, involved in the interpretation of the data obtained. In the first place, have we controlled the complete environment? Light and total darkness, air temperature, humidity, evaporation rate, vibration, wind movement have been held constant; recently (Horstmann 1935) the electrical changes in the atmosphere have apparently been eliminated and environmental infra-red radiation (Park 1937) removed. Food and water supply and the excessive accumulation of faeces offer no major difficulties with the newer recording equipment. Ultra-violet is not involved in totally dark cabinets and water screens. There remain cosmic rays and certain other little understood influences, for example, periodic changes in the gravitational and geomagnetic fields.

The perfect experiment has not been performed. It would include recording apparatus, the records of which are changed without disturbing the experimental animals; food and water supplies similarly handled; cabinet control of light, temperature, and humidity well within the limits of experimental error; lead walls to eliminate environmental infra-red; the whole experimental equipment operated in some deep cave (300 to 400 feet under ground) to eliminate cosmic rays; the experimental animals reared apart from their parents to eliminate direct or indirect tutoring, and reared in the experimentally constant environment to eliminate habit formation.

The writer is convinced that the periodic activity patterns demonstrated under controlled conditions are not the product of the immediate environment, but are internal and resident within the organism. Such periodic activity patterns have been placed in a second category of activity by the writer, namely the Endogenous Type of Activity. These periodic patterns have been given other names (vital rhythms, inner rhythms, internal, endogenous, inherent, innate, etc.), but the designation eventually adopted is of little consequence as long as such activity patterns are distinguished from those of the environmental type, and we differentiate between *inherited pattern* and habit (cf. Park 1940a).

Recently the training of insects, and the subsequent analysis of this habituated activity, has received renewed attention. These investigations are pertinent to the general problem since they serve to emphasize the importance of separating habit-formation from true periodicity. Following the early lead of Beling (1929) that the activity of bees appeared to have a twenty-four hour rhythm of feeding, Grabensperger (1933) found that ants and termites could be trained for a feeding rhythm of a particular temporal character. Ants appeared to be easily trained, viz. they were very plastic. Their experimental feeding rhythm would endure for nine days after the food was

removed from the feeding chamber; termites could be trained to a twenty-one hour rhythm. Grabensperger (1934, 1934a) then used a variety of chemical compounds with the food and found a number of resulting changes in the feeding pattern established experimentally. For example, using bees and wasps it was found that quinine delayed, and iodothyreoglobulin tended to accelerate the feeding time. Kalmus (1934) was able to train bees to visit a given feeding place at a certain time and found that certain influences modified the experimentally induced habit (low temperature, carbon dioxide, quinine) while others (etherization, prolonged darkening of the hive) did not appreciably affect the habit. Kleber (1935), in an ingenious paper, reported similar training of bees, and then studied the relation of the normal feeding rhythm of bees to the pollen and nectar production of a number of flowers. Kleber suggests that the normal feeding rhythm of bees may be a naturally formed activity pattern, just as the experimentally induced feeding rhythm is a humanly formed habit. All of these researches tend to differentiate between the environmental induced habit ("time sense" of certain authors, but not of all who use this term) and the internal periodic patterns which are initiated within the organism as a deeply seated response.

The distinction between exogenous and endogenous rhythms, however, must be understood. A more complete understanding will only come with continued investigation, but it seems obvious that a periodic phenomenon is either induced by the environment or is not so induced. Those patterns induced by the immediate environment are environmental, while those induced by the internal environment are internal. These patterns may be a consequence of (a) former induction by a rhythmic environment within the life of the individual, that is, habit formation, or (b) truly inherent. This question of habit *versus* inherence is an important aspect, but can be resolved by further research upon the immature or young stages of animals. Thus, in the beetle, *Boletotherus cornutus*, the beetles of one experimental series were raised from the egg stage in the fungi, in light-tight containers, and the activity pattern of these adult beetles was in general that of other beetles collected from fungi in the forest when adult (Park and Keller 1932).

Again, there is the question raised by the modifiability of the true inner rhythm by the environment. The experimenters cited in Table 5 varied their investigations in a number of ways; in some cases constant darkness, constant light of various intensities, or light and dark periods of many different lengths of time were employed; the twenty-four hour cycle was reversed in other experiments, exposing the animals to a dark day and an illuminated night; similarly starvation or regular feeding; varying the temperature or varying the relative humidity, have been used in certain experiments. The details of these investigations can be learned by consulting the literature cited. From a study of these there emerges a clear conclusion: namely, that the rhythm can be modified by the environment. But this conclusion is not new. We

are unfamiliar with any protoplasmic property which may not be destroyed or altered by the environment. That protoplasm and protoplasmic rhythms are modifiable would seem to be well established and of long standing. On the other hand it appears remarkable that such rhythms can persist in the face of such abnormal conditions (cf. Park and Keller 1932, Park 1935) and the writer's view of the internal periodicities of protoplasm coincides with the observations of others. It has been repeatedly pointed out (Park 1935) that the existence of periodism of activity should not be confused with modification of the rate and character of this periodism by environment. This is obvious, since organismal periodism in the whole community must keep step with the gradual change in the environment, for example with the change in light intensity with time of year and latitude or altitude; it is suggested by the known modification of environmental influence upon activity *(vide supra)*; it has recently received experimental confirmation by Johnson (1939). Johnson found that white-footed mice *(Peromyscus)* had a well-defined activity rhythm which persisted in constant conditions for eighteen months, but that the rhythm could be shifted through the twenty-four hours and that definite amounts of modification of the activity result from definite light intensities. Again, within the organism such rhythms as the beat of the reptilian heart can be experimentally altered or destroyed (Chu and Sollmann 1925, 1925a, 1925b), and this modification of activity does not cause one to assert that there is no cardiac rhythm.

There are a great many such physiological rhythms, some not as fully investigated as the cardiac rhythm, but all of interest since these periodic phenomena within the organism are partially responsible for, or arise in part from similar sources as, the ecological activity rhythm of a whole organism. Consequently study of rhythmic phenomena is one of the many fields in which both physiology and ecology can cooperate for a solution of a common problem. Such functional rhythms range from the rate of deposition of dentin and enamel in rat incisors (Schour and Hoffman 1935, 1935a; Schour and Steadman 1935) to the periodic migration of pigment in the eyes of crustaceans (Welsh 1930, Bennitt 1932, *et al.*).

Thus there are many insects (certain Diptera, Lepidoptera and Hymenoptera especially) which show a remarkable constancy in the emergence of adults from the pupal cases. As with activity patterns, such emergence is characteristic of a given species, the period of the twenty-four hour cycle in which emergence occurs varying between different insects but remaining relatively fixed for members of the same species. Bremer (1926) used a variety of flies and their hymenopterous parasites, as well as a meal moth. In general he found that light was an important modifying influence. However, the meal moth *(Ephestia kühniella)*, which under normal day-night sequence shows 95.3 percent emergence between 2 P.M. and 5 A.M., and only 4.7 percent emergence from 5 A.M. to 2 P.M., continued to emerge at

practically the same times when in constant darkness. Bünning (1935) studying the emergence of *Drosophila,* found that external changes even during the early embryonic stages have little effect on the emergence rhythm, and that after fifteen generations of *Drosophila* were kept in constant light, temperature and humidity, they still exhibited the emergence rhythm. Kalmus (1935) attaches great importance to light intensity in the control of *Drosophila* ryhthm of emergence, but in constant darkness obtained a relatively typical pattern.[1]

Bünning also demonstrated that the rhythm of emergence could be lengthened by lowering the temperature and shortened by increasing the temperature, as he had previously demonstrated for physiological rhythms in bean plants *(Phaseolus),* and Bünning pointed out that this temperature control of the rhythm makes its inherent character the more obvious. Certainly these results with temperature coincide with the effect of temperature upon the velocity of cardiac and other inherent physiological phenomena.

Kalmus (1935), however, introduces a different idea from that held by the majority of workers in this field. He separates environmental and inherent patterns on the basis of velocity, thus those functions which have their velocity influenced by environmental factors he terms *allochronous,* while those which endure without such modification are called *autochronous.* Such a restriction of inherent (autochronous) rhythms would not agree with the view set forth in the preceding pages; nor with the view of many other investigators.

Horstmann (1935) kept pupae of nocturnal lepidopterans in darkness for from two to ten days prior to emergence, and when the adults emerged he found the same periodic migration of pigment in their ommatidia as that experienced in the ommatidia of normally reared forms. This, too, is a clear case of a deeply-seated physiological rhythm; however, Horstmann attributes the persistence of the pigment rhythm to a memory of the larval period, a view which cannot at present be justified by experimental data.

Within the last ten years a large body of information has been accumulated upon physiological rhythms, and the relation of the induction or maintenance and modification of these periodic phenomena to the endocrine secretions. Among numerous examples, in addition to the role of hormones in the rhythms associated with the bird and mammal reproductive systems, there is the apparently extensive control of pigment in Crustacea by secretion of hormone or hormonoid materials. This paper does not pretend to review these and other physiological rhythms. They have been given admirable at-

[1] Unpublished observations of the writer indicate the same rhythm of pupation in another fly. While studying the guests of the mound-building ant *(Formica ulkei Emery),* a number of the slug-like larvae of the syrphid fly *(Microdon)* were obtained (Park 1935) and reared to adults. These adult flies belong to an undescribed species and emergence of the adults from the puparium always took place in the night, especially the hours preceding dawn. My data on emergence, however, are observational only and are not critical in the sense that rigid experimental conditions were maintained. *Microdon* emergence, however, should be examined experimentally, especially since the pupation takes place in the relatively constant environment of the host and nest.

tention by others (Bouvier 1922, Chap. III, Richter 1927, Rau and Rau 1929, Kalmus 1935, Hoagland 1935, Hemmingsen and Krarup 1937, Jores 1937, and Welsh 1938). It should be pointed out, however, that since so many internal cycles have a secretory control, and since total activity is partially an expression of internal physiological states, inherent activity patterns are affected by these internal conditions, and later research may show that such inherent activity is induced by rhythmic secretion. On the other hand were such a direct connection between activity and secretion established, it would merely raise the question as to the nature of the stimuli which induce such periodic changes in the endocrine system.

Consequently, whether we are dealing with inherent activity, or with internal physiological cycles, the problem of the general inherited pattern of protoplasms is eventually encountered.

Before discussing the nocturnal problem as a whole, there is a third category of activity which must be examined.

ARHYTHMIC ACTIVITY

From what has been said it is clear that the generally accepted view of physiologists regarding activity and inactivity is insufficient to explain the facts accumulated, nor are ecologists in a more enlightened position. In addition to the types of activity patterns reviewed, there are other species, relatively few in number, which have no fixed pattern of activity. That is, individuals of such species satisfy their physiological requirements at any period of the twenty-four hour cycle. It follows that such species have no discernible day-night periodicity, and consequently activity tends to be distributed over day as well as night. This is not to say that individual habits may not be fixed in a given individual or group of individuals. On the other hand, in certain of these arhythmic forms a very plastic behavior has been demonstrated, and habits can be induced which give to the animal a superficial resemblance to the patterns of animals in the exogenous or endogenous categories. Close observation and controlled experiments are quite necessary to differentiate this activity type. Thus under constant conditions, the *exogenonts* are active or inactive as a group, depending upon the conditions being maintained with respect to their normal pattern; the *endogenonts* tend to maintain the activity pattern regardless of the constant conditions; the arhythmics present no group action, some individuals being in activity at any section of the twenty-four hours. It should be pointed out that such constant conditions must be held well within the limits of toleration of the species concerned.

One generalization which can be made of the arhythmic group is that they inhabit constant environments, or are social forms. Examples of this category include the cave crayfish, *Cambarus pellucidus*, the log-inhabiting,

relatively social beetle, *Passalus cornutus,* certain ants, certain termites and modern civilized man.

Results upon *Cambarus pellucidus* are so recent (Park, Roberts and Harris 1940) that no extensive comment is necessary. It was shown that under constant darkness, constant illumination of several intensities, reversed illumination, or normal day and night variation, at constant temperatures, well-fed males or females of these cave crayfishes gave an arhythmic pattern of activity. Each crayfish was active or inactive individually and independently. This species, although lacking the pigmented eyes of its epigeous congeners, is photonegative and consequently gives a more intense record of activity in illuminated experiments, but the distribution of activity, that is, the percentage of active to inactive time, is relatively equally divided between the day and the night. Such a distribution for a species population is an index of its arhythmic nature (cf. Park 1940a).

Similarly the black passalid beetle, *Passalus cornutus,* shows a truly arhythmic activity under a wide variety of conditions varying from normal to highly abnormal environmental conditions (Park 1935, 1937), and although activity is increased under unfavorable, low relative humidities, the distribution of time active and time inactive is uniform and roughly equally divided between day and night.

The normal environments of both the cave crayfishes and log-inhabiting passalid are constantly dark, and the temperature and other conditions relatively stable and uniform, in contrast to the external environment. Both of these species have been studied by means of recording equipment under controlled conditions, and the activity analyzed for its percentage distribution over the twenty-four hour cycle. The data accumulated on the social species is more circumstantial, but never the less suggestive.

That certain species of ants have no uniform period of inactivity appears to be well substantiated. Thus McCook (1877) speaking of eastern mound-building ants observes:

> ants at Camp Riddle, when observed during every hour of the night from sunset to sunrise, were found to be pursuing the very same labors in the same way, and in the same fields as during the day. The avenues, tree-paths, feeding stations, feeding grounds and hills were always thronged day and night.

This clear statement by an experienced myrmecologist regarding the normal activity pattern of *Formica exsectoides* is convincing. Parallel observations are numerous. *Lasius niger americanus* (Flint 1914), *Aphaenogaster fulva* (Park, Lockett, and Myers 1931), *Aphaenogaster fulva picea, Aphaenogaster tennesseensis, Camponotous caryae,* and *Camponotus herculeanus pennsylvanicus* (Park and Strohecker 1936) have also been observed through day and night, and species activity appears to have been constant. It is to be expected that in such species the active periods were at different times for

different individuals; probably there was greater activity during certain periods of the twenty-four hour cycle, but the distribution of active to inactive periods appears to resemble, very closely, that of passalids and cave crayfish. Flint's observations (1914) were substantiated (Park and Strohecker 1936), these "corn field ants" appearing at observation stations at all times of the day and night. Seeman (1928) found that *Crematogaster lineolata* worked through the night, even during rain and thunder storms, while *Formica pallide-fulva* he found more active by day than at night. This same arhythmicity was found by Schneirla (1938) for the army ant, *Eciton hamatum* in the Barro Colorado rain forest. Schneirla found that during the nomadic phase of colony activity there was vigorous raiding throughout the day with morning and afternoon peaks of activity, and the raiding was usually continued during the night, but less vigorously; during the statary phase the army ants raided much less vigorously during the day, and nocturnal raiding was weak or absent. Mallis (1938) observing army ants in California found this same nocturnal raiding taking place, so that it appears that many ecologically different ants, belonging to widely separated taxonomic categories, regularly continue to practice their colony activities over the twenty-four-hour period.

The activity of termites in this regard is unknown. Andrews (1911) reported that certain Jamaican termites were active at night. The arhythmicity of oviposition of termite "queens" is apparently substantiated, the queen laying her eggs through the day and night in an unbroken stream. On the other hand, the production of alates and the colonizing flight are periodic. The latter seems to be primarily correlated with the periodicity of rain. Both a field and an experimental analysis of activity of these highly social animals is needed from the point of view of the activity pattern they possess.

There seems to be little doubt that man is arhythmic, or at least the human species has no inherent pattern of activity. In the long polar nights or days the Eskimos have highly irregular periods of activity, and of eating and sleeping (Pearse 1926). The fact that man forms habits easily may give a superficial appearance of periodicity. No uniform type of twenty-four hour variation was found in a study of energy expenditure and performance (Freeman 1935) which again confirms human arhythmicity. In an important experimental study of the activity of human infants, Szymanski (1918b) using recording equipment found that infants were polyphasic, viz. had more than one large activity period and more than one inactive period over the twenty-four hour cycle. Szymanski viewed his findings as demonstrating that the adult human depends upon the sense of vision to a great extent, and hence becomes secondarily a diurnal, monophasic organism. Szymanski (1922) later continued his research on human activity, confirming his earlier view as to the monophasic character of adults. He found in general that the ratio of activity to rest was a fairly constant one, and our common experience of

modern human communities impresses us with the ability of man to adapt his rest and activity periods to the exigencies of his particular occupation and the demands of his diverse avocations. Kleitman (1937) found that during the first year of life, the human infant's range of body temperature was gradually established; during the second year of the child's life, the adult type of body temperature curve becomes definitely fixed. The relation of the body temperature curve to the curve of activity and inactivity is generally close. This lends to human activities a distinct resemblance to the purely endogenous type of activity.

The apparent arhythmicity of such social species is interesting. It suggests that the society, in basing its existence upon mutual cooperation, places in operation a system of demands upon the individuals composing the aggregate. These demands can be satisfied only by ignoring the rhythmic natural sequence of the twenty-four-hour cycle, and consequently a purely physical periodic environment is replaced with a relatively constant social environment. Under the social system some individuals are active regardless of when a sample is taken. If this is true, social life may not flourish save in species with a highly plastic behavior. If the social medium is regarded as a relatively constant influence, then the conclusion emerges that arhythmicity is a correlative of constant environments. Thus such highly social forms as ants, man, possibly termites, and on the other hand log-dwelling passalids (which are definitely semi-social) and cave crayfish resemble each other in the relative constancy of their particular habitats. Apparently the more periodic activity-inactivity cycle of other social Hymenoptera, such as the bees and wasps, is an exception to the view given above and this aspect of the problem has been treated recently in a theoretical paper on community symmetry (Park 1940).

THEORETICAL DISCUSSION OF THE GENERAL PROBLEM

Students of animal distribution have not given sufficient attention to the bearing of activity pattern upon the problems of biogeography. Isolated suggestions have been made, often by investigators whose research interests lay elsewhere; these ideas should be interwoven to present the nocturnal aspect of zoögeography. The view of Clark (1914) has been discussed recently (Park 1938), but it should be noted that Clark held that such typical nocturnals as elephant, hippopotamus, tapir, sloth, various edentates, many lemurs, non-aquatic monotremes, geckos, onychophores and diplopods are found either abundantly or exclusively in the equatorial rain forests; that where there is relatively little imperfection in the geological record, such nocturnals are shown to have a long palaeontological record and that these forms are more archaic than diurnal types. Here is a zoogeographic suggestion that nocturnals are more primitive than diurnals, and are notably present in abundance in the rain forests. This general view is partially expressed

again by Barbour (1926, p. 8) for certain reptiles. The ecological geography of nocturnality will necessarily emphasize the essential difference between nocturnal habits in hot deserts, where they are conditioned by the extremes of the physical environment and such habits in a tropical rain forest, where we may interpret them as due to the competition of a rich fauna. In a stimulating theoretical paper, Kennedy (1928) discussed the geographic, seasonal and twenty-four hour distribution of the insects in relation to their phylogeny. This paper brings forth substantial evidence that primitive insects have lower rates of metabolism than modern insects; that the tropics have a greater energy intensity than boreal regions, the hot and illuminated day a greater energy intensity than the cool and dark night. Thus the primitive forms usually occur in cool, darkened habitats such as deep forests or are nocturnal, or both, while more modern orders tend to be diurnal. The exceptions are naturally numerous, but the general point of view agrees with that of others, namely that modern relics of primitive groups are more apt to be nocturnal, and are often tropical. Rau (1929) after working with saturniid moths and finding certain species with a deeper-seated activity rhythm than other species, concluded that the form with the more deeply seated nocturnal pattern was phylogenetically older than a species with a less deeply seated activity pattern. Although such a criterion of phylogenesis may not prove true for unrelated groups of organisms, it may be admissible for closely related forms within a common group. It again reflects the view that phylogeny and activity patterns, and hence distribution of the activity periods, whether deeply seated or not, may be related. Walls (1934) in a study of the reptilian retina, presents histological evidence over a wide range of material to substantiate his view that many groups of modern reptiles have become nocturnal secondarily. This change in activity pattern, according to Walls, has nearly always been accompanied by a transmutation of all or some of the cones of an ancestral diurnal and pure-cone retina into a nearly or wholly pure-rod retina adjusted for nocturnal vision.

From the separate ideas there emerges the view that nocturnalism is a specialization which arises from an original diurnal stock, and that the existing nocturnal forms are generally more primitive than the modern diurnal groups. This phylogenetic consideration can be tested in the study of animal distribution, but the application must be in the hands of zoögeographers skilled in the details of distribution of special groups of animals. The Matthews theory (1915) of the more modern and consequently more effectively adjusted species at the center of the dispersal area, and the more primitive and less effectively adjusted species at the periphery of the dispersal area, may be combined with this view of primitive nocturnality and modern diurnality. If such a combination proves sound, we should expect to find either the primitive forms at the center of the dispersal area, as nocturnal species to avoid competition; or the primitive stocks distributed peripherally and either

preponderantly nocturnal, or diurnal according to their subsequent history in the new environment. Light would be cast on this precise point by a general review of the habits of the Madagascan lemurs. The Central African and Asiatic lemurs are notably nocturnal forms, thus evidently escaping the main biotic pressure of the rich associated fauna. The Madagascan lemurs, without the competition of the modern carnivores, might be expected to exhibit a higher proportion of diurnal forms.

There are other problems, relating to the evolution of activity pattern. It is obvious that the world environment is rhythmic, which fact can serve as our point of departure for an analysis of biological periodism. We have found that environmental periodism and biological periodism are synchronized, but is this correlation apparent or real? It has been previously and repeatedly held that this is a real correlation, in fact that the environmental rhythmicity has been the cause of biological rhythmicity (Reynolds 1920, Bouvier 1922, Welsh 1938). This assumption is very plausible, but the argument should be critically examined and if possible carried further.

Circumstantially, when we survey the problem ecologically we find that where the environment is rhythmic, the organisms inhabiting the environment are rhythmic in their major activities. Since an organism must adjust to prevailing conditions, migrate or die, we view the extinction of species as a failure to adjust, or move into the relatively few constant habitats. These species have been replaced by more plastic forms, or by others whose adaptations allowed survival.

We have seen that the periodic environment of temperate regions is characterized by numerous adaptive biological rhythms, such as hibernation and aestivation, close phenological correlation of leafing, fruiting and reproductive cycles of animals, lunar cycles, and periodic activities within the twenty-four hour cycle.

Where the annual seasonal cycle is incompletely defined, organisms do not show such uniform periodism. In the tropical regions (Flattely 1920, Visher 1923, Haviland 1926) there is a conspicuous individuality of breeding, leafing and flowering. In these regions, day and night are relatively constant and there is a marked periodicity of those activities associated with the twenty-four-hour cycle (Park 1938, Park, Barden and Williams 1940).

With reference to this cycle of day and night, we have presented evidence for (1) an exogenous activity pattern, (2) an endogenous activity pattern, and (3) an arhythmic activity. It should be noted that the first two may be combined in many species as (4) a composite activity pattern, and both of these first two patterns may be phylogenetic stages of development of a deeply-seated pattern of activity. The first type has its character induced by environment, the second type is more deeply seated and is continued for a greater or lesser time depending upon the degree of stability of the pattern, and secondly, the tolerance threshold for adverse conditions.

Here, then, is a consistent view of nature, built upon a frame-work of centripetally arranged and overlapping periodicities. There seems to be a sufficient body of evidence to postulate a causal relationship between environmental and biological rhythms over geological time. If such a causal assumption is made, how has the induction taken place? Our position is that biological rhythms have been selected by the rhythmic environment, operating upon mutations which have a positive adjustment value. Protoplasmic inheritance is not necessarily limited to morphological features. Pincus (1931) mated a strain of dilute brown mice with white mice. Both strains had different relations of frequency of respiratory movements to body temperature. The F_1 hybrids of this cross exhibited the relation of respiration to body temperature of one or the other of the parents, not a blend of the two parental relations. Consequently the hybrids inherited the value of the constant unchanged from one parent. This is the inheritance of a purely physiological character. Mutation pressure might well be maintained in the direction of periodic activities, in an environment which placed a survival value upon such periodic patterns.

Furthermore, a natural laboratory is at hand. So far we have been considering the rhythmic environment, but there are at least three relatively constant environments, namely caves, abyssal communities, and complex societies. Caves and abyssal regions are essentially inorganic, but the social matrix is essentially biological. At the present time the experimental investigation of the sea deeps is not feasible. We are led to believe, however, from data accumulated that they present a vast and relatively constant area (Coker 1938), although certain recent data (Livingstone 1937, Welsh, Chase and Nunnemacher 1937) indicate vertical migrations of certain moderately deep water forms over the twenty-four hour cycle. The problems concerned with the activity patterns of true abyssal species are of theoretical importance, but there are insufficient facts at present to warrant discussion of the question.

Caves, on the other hand, are accessible, and the biology of subterranean forms is attracting increasing attention. From the viewpoint of periodism, cavernicoles are perfect experimental material. Regardless of the manner in which caves have been colonized, existing cave forms mark the end product of a natural experiment, an experiment with the beginning lost in geologic time. The control for this natural experiment is the adjacent, phylogenetically related, epigeous stocks. The cave environment is a constant habitat, not only as to such obvious influences as darkness, temperature, relative humidity, evaporation rate and air movement, but for such lesser known possible factors as cosmic radiations. The food-supply is meager and may be periodically enriched with vernal foods in some caves; in large caverns, such as Mammoth Cave of Kentucky, many species of animals have existed for thousands of years in a remarkably stable habitat.

Activity of cavernicoles has hardly been touched, with the exception of the cave crayfish. If what we have postulated concerning the origin of

biological rhythms is tenable, any cavernicole which is shown to have an inherent activity pattern will acquire new importance. Demonstration of such a rhythm would attest to the tenacity of the activity pattern after many generations in a constant environment in which a day-night periodism would appear to have little positive survival value. At the present time I do not know of such a demonstration, but the research value of such an attempt is high. The arhythmic pattern of a cavernicole, when present, may suggest either a loss of periodism, or a lack or insufficiency of pattern in the original stock which presumably entered the subterranean habitat and escaped competition in a populous periodic environment. Colonization of caves has been progressing, in all probability, for a long period of time and at different rates, and is probably continuing at the present time. The examination of activity patterns should offer another tool by means of which cave biology may be advanced. Habit, at least for all save the chance cavernicole, can be eliminated in an activity pattern here, and since the constant environment is normal for the species, inherent patterns if they exist could be readily demonstrated, under constant laboratory conditions.

It seems therefore, that study of nocturnalism and its inter-relations is a comprehensive biological program, the working out of which may further illuminate such problems as organismal periodism, environmental adjustment, vision, protective coloration, sleep, social life, zoögeography, and phylogeny.

At the turn of the century the anatomy of cave animals was being studied; Howard and others were observing the flight of insects at night; Verrill was speculating on the protective value of color patterns at night; the effects of weather upon activity were being observed, and Dubois and Kiesel were studying internal physiological rhythms. Later, the rhythms in protozoan reproduction and their relation to experimental environmental conditions were being investigated by Woodruff and his students. It was some twenty years before Szymanski was to employ recording apparatus in a general study of activity; thirty years before either controlled ecological experiments on activity, or the study of nocturnal parts of communities, or exact experimental demonstration of internal rhythms as a function of definite physiological states. The problem is much more clearly seen now. Certain questions have been answered, new questions have arisen through the progress of research. These new questions must be tested externally by ecologists, internally by physiologists, and the inheritance of innate functions analyzed by geneticists before the full meaning of nocturnalism can be appreciated.

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